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Iowa State University of Science and Technology
Ph.D., 1966
Agriculture, forestry and wildlife

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PHOTOSYNTHESIS, RESPIRATION AND GROWTH OF SCOTCH PINE SEEDLINGS

by

John Charles Gordon

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Major Subjects: Silviculture
Plant Pathology

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Heads of Major Departments

Signature was redacted for privacy.

Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa

1966

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INTRODUCTION

Scotch pine (Pinus sylvestris L.) is being planted extensively in Iowa and elsewhere in the United States, and has the largest natural range of any commercially important tree species. To aid in the selection and breeding of Scotch pine for specific production goals, the existence and magnitude of genetic variation in physiological processes within the species should be known, and the relationship of such variation, if it does exist, to intraspecific growth variation should be determined. The physiological response of Scotch pine to different levels of environmental factors is also important, even in the absence of intraspecific variation, if an optimum plant-environment relationship for a given production goal is to be created.

The probability of detecting physiological variation within a species should be roughly proportional to the extent of its natural range, because more widely ranging populations will have been exposed to a greater range of selection pressures. Because of greater intraspecific variation in wide-ranging species, the selection of variants for specific production sites and goals must be more rigorous. Rigorous selection requires detailed knowledge of both the inherent growth and physiological variation pattern and the more general responses of the species to environmental factors.

Because Scotch pine exists over a broad latitudinal range, and shows a differential response to daylength among seed sources (Jensen and Gatherum 1965), and because photosynthesis is a light-controlled process, rates of photosynthesis and growth should vary with latitude of seed

source, when seedlings from different latitudinal sources are grown in a common environment. Because photosynthesis is an important yield determining process, variation in rates of photosynthesis should affect the productivity of the seed sources in the common environment. If variation in rates of photosynthesis exists, and the relationship of photosynthesis to growth can be elucidated, measurements of rates of photosynthesis could be used, with other criteria, to develop rapid selection methods. Since light intensity, CO_2 concentration and temperature are the most important external factors affecting rate of photosynthesis, specific effects of these variables on rate of photosynthesis in Scotch pine and the extent of their interaction with each other and with genotype should be known. Respiration also is an important yield determining process and may be affected by the same factors affecting rates of photosynthesis. Therefore, when rates of photosynthesis are measured by CO_2 exchange, rates of respiration should be measured.

For these reasons, Scotch pine seed was obtained from different European seed sources over a wide range of latitudes and a narrow range of longitudes, and controlled-environment studies were conducted to (1) test differences in rates of photosynthesis and respiration, and growth and distribution of assimilate among seed sources, and (2) determine the effects of light intensity, CO_2 concentration and temperature on rates of photosynthesis and respiration. The specific objectives of the studies were (1) to determine the magnitude of differences among seed sources in growth and distribution of assimilate when grown in a common environment, and to determine the relationship of such differences

to latitude of seed source, (2) to test for among-source differences in rates of photosynthesis and respiration, and to determine the relationship of such differences to latitude of seed source, (3) to define the relationship between selected levels of CO_2, light intensity, and temperature, and rates of photosynthesis and respiration, and (4) to detect interactions between environmental factors and latitude of seed source in their effects on rates of photosynthesis and respiration.

REVIEW OF LITERATURE

Growth and Distribution of Assimilate

Effect of seed source

Intraspecific variation in Scotch pine has been under investigation for over a century. A concise review of the earlier investigations of growth variations within the species is presented by Echols (1958). Early work indicated that the source of seed affected response to environmental conditions and growth habit. Langlet (1936) was the first investigator to present a general theory, with supporting data, describing the genetic variation pattern within the species. He observed a progressive north to south series in measurements of several characters, including growth rate, in seedlings grown in Sweden from seed collected from 97 sites across the Swedish latitudinal range of the species. He concluded that variation in all of the characters measured was continuous, and that therefore Scotch pine exhibited only clinal genetic variation in response to the major climatic gradients across its range. Subsequent to Langlet's investigations, the effects of seed source on growth, survival and other characters were studied systematically by a number of researchers. Echols (1958) summarized Langlet's (1943) compilation of north-south trends. According to Langlet, seedlings will exhibit differences, with the northern sources showing, in comparison to the southern:

1. Better overwintering capacity
2. Greater resistance to parasitic fungi

3. Earlier beginning of growth in the spring
4. Earlier cessation of growth in the autumn
5. Less total annual height growth
6. Straighter stem form
7. Fewer, shorter and weaker branches
8. Shorter, broader and thicker needles
9. More sugar, fat and catalase, but less water and chlorophyll in the needles in winter and autumn.

Wright and Baldwin (1957), reporting the results of the IUFRO Scotch pine provenance test in New Hampshire, divided the range of Scotch pine into ecotypes on the basis of height growth, and thus challenged Langlet's clinal theory. Langlet (1959) took exception to Wright and Baldwin's interpretation of their data, and reasserted that variation within the species was solely clinal. Using trees from the same New Hampshire provenance test reported by Wright and Baldwin, Echols (1958) found a significant curvilinear relationship between latitude of seed source and tracheid length, and a less pronounced relationship between seed source and wood density. Gerhold (1959), also using trees from the New Hampshire provenance test, found two Scandinavian provenances to be high in boron, nitrogen, and carotenoids, and low in iron and chlorophyll, on the basis of fall foliar analyses. Differences in fall color found by Gerhold could not be removed by fertilization and were therefore deemed genetic.

Wright and Bull (1963) reviewed literature reporting geographic variation in Scotch pine and reported the results of a 3-year, 122-

seed lot, provenance test in Michigan. They found trends in growth and morphology supporting Wright and Baldwin's division of the species into ecotypes. They also found most apparent adaptive trends to be north-south (latitudinal). These trends are summarized below:

1. Most rapid height growth and greatest needle length occurred in progenies from central Europe; southern and northern provenances grew less rapidly and had shorter needles
2. Seed size increased from north to south
3. Date of the first year bud set was progressively later from north to south
4. Two-needled clusters appeared first on northern progenies and later on southern progenies
5. Northern progenies exhibited greatest winter color change
6. Trees from the extreme north and south were more difficult to pull from the ground than those of intermediate provenance.

The authors also offered an explanation of the evolution of Scotch pine ecotypes. West and Ledig (1964) found a significant difference among seed sources of Scotch pine in the amount of lammas shoot formation. Stout (1964) investigated stem-crown relationships in several seed sources of Scotch pine and found the relationships varied significantly among seed sources.

Wright and Bull's conclusions do not differ greatly from those

of Langlet, except as to whether intraspecific variation in Scotch pine is ecotypic or clinal. Latitudinal trends in some characteristics of Scotch pine are well established, and such trends appear when seed from several latitudinally disparate origins is grown in a common environment. Inasmuch as temperature during growth and photoperiod have been shown to affect the growth of Scotch pine seedlings from different seed sources differentially (Wareing 1950, Jensen and Gatherum 1965), it appears that Vaartaja (1954) was right when he hypothesized the existence of photoperiodic ecotypes of Scotch pine. Vaartaja suggested that these ecotypes, modified by temperature, have arisen through natural selection in adaptive response to latitudinal daylength and temperature gradients.

Photosynthesis and Respiration

Effect of seed source

The effect of seed source on rate of photosynthesis in Scotch pine seedlings has been investigated by Gordon and Hagman (1966)[1] who found greater photosynthesis per unit fresh weight of top, but less total photosynthesis, in seedlings from a Lapland seed source than in seedlings from more southerly seed sources. The effect of seed source on photosynthesis and respiration in conifer seedlings of other species has been studied by McGregor *et al.* (1961), Krueger and Ferrell (1962), and Bourdeau (1963). McGregor *et al.*, using 1-year-old loblolly pine seed-

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[1]Personal communication from Max Hagman, Forest Research Institute of Finland, Helsinki, Finland.

lings, found a difference in net photosynthesis between Georgia and Florida seed sources, with the difference accounted for by a corresponding difference in quantity of photosynthetic tissue. Krueger and Ferrell found differences in photosynthesis and respiration between Douglas fir seedlings from Rocky Mountain and Coastal seed sources. Bourdeau found that eastern white pine seedlings from southern seed sources were more efficient photosynthetically in weak light and had lower compensation points than those of northern origin, but that the southern sources were less efficient at low temperatures. Bourdeau concluded that genetic variability in photosynthetic and respiratory responses exists in white pine, but appears only under certain combinations of treatment and environmental conditions.

The effect of genotype on photosynthesis and respiration has been investigated by Huber and Polster (1955) in poplar clones, by Bourdeau (1958a) in male and female aspen, by Bjurman (1959) in diploid and tetraploid gooseberry, by Bourdeau and Mergen (1959) in polyploid slash pine seedlings, by Rusch (1959) in poplar clones, by Mooney and Billings (1961) in geographic variants of Oxyria digyna, by Polster and Weisse (1962) in larch, by Kendall and Taylor (1963) in clones of red clover, and by Tonzig and Marre (1964) in poplar hybrids. The data indicate that genotype can affect photosynthesis in two ways; (1) by determining the quantity of photosynthetic tissue produced or (2) by determining the efficiency (CO_2 fixed per unit tissue per unit time) of photosynthetic tissue. Efficiency may be changed by gene-controlled differences in leaf shape, leaf arrangement, internal structure, or

biochemical constitution. Respiration appears to be affected similarly by genetic factors. Because respiration may differ in light and dark (Decker 1957, Krotkov et al. 1958), and only dark respiration can be readily measured, the relationship between genotype and respiration during photosynthesis is unclear.

Effect of environmental factors

The effect of light intensity on rate of photosynthesis in Scotch pine seedlings has been investigated by Stålfelt (1924) and Decker (1954). Stålfelt found a linear relationship between rate of net photosynthesis and light intensity up to one-third of full sunlight, and a more gradual increase up to full sunlight. Decker found a positive, linear relationship between light intensity and rate of net photosynthesis in the range of 1,800 to 6,400 foot-candles. Earlier, Kramer and Decker (1944) found that photosynthesis in individual loblolly pine needles was saturated at one-third of full sunlight, but that whole seedlings achieved maximum rates of photosynthesis only at full sunlight. The difference between saturation intensity in individual needles and whole seedlings was ascribed to mutual shading of needles on seedlings. The effect of light intensity on photosynthesis and respiration in trees of other species has been investigated by Wassink et al. (1956), Kozlowski (1949, 1957), Bourdeau (1958b), Pavletic and Lieth (1958), Negisi et al. (1961), Clark (1961), Sirois and Cooper (1962), and others. It is commonly held that the so-called intolerant pines do not reach light saturation of photosynthesis until full sunlight intensities are reached, if then. It is assumed that hardwoods, at least those tolerant of shade, reach photo-

synthetic light saturation at intensities equivalent to one-third of full sunlight (Kramer and Decker 1944, Kramer and Kozlowski 1960). General discussions of the analytics of photosynthesis vs. light intensity curves may be found in Rabinowitch (1951), and Thomas (1965).

Freeland (1944) reported photosynthesis in Scotch pine at -6°C. Iwanoff and Kossowitch (1929) found that photosynthetic activity of Scotch pine decreased sharply during winter. The effect of temperature on photosynthesis and respiration of other coniferous species has been investigated by Clark (1961), Stålfelt (1924), Decker (1944), Tranquillini (1955), Pisek and Rehner (1958), Pisek and Winkler (1959), Pharis and Woods (1960), Parker (1961), and Negisi and Satoo (1961a). In most coniferous species studied, maximum net photosynthesis occurred in the range of 10 to 25°C, with more northerly species reaching maxima in the lower half of the range. As temperature rose above 0°C, the net photosynthesis to dark respiration ratio decreased.

The effect of atmospheric CO_2 concentration on rate of photosynthesis in Scotch pine was investigated by Stålfelt (1924). He found that photosynthesis increased if CO_2 concentration was increased above the normal atmospheric concentration, but that high concentrations were injurious. No information is available concerning the CO_2 compensation point of Scotch pine seedlings. Negisi and Satoo (1961b) found a linear relationship between CO_2 concentration and net photosynthesis in the 220 to 330 ppm range, for two Japanese tree species. Rabinowitch (1951) and Thomas (1965) present general reviews of the effect of CO_2 concentration on rates of photosynthesis. Decker (1959) discusses the concept

of CO_2 compensation point.

For a more comprehensive review of the effects of environmental factors on photosynthesis in trees, see Kramer (1957).

CO_2 Exchange and Growth

Baker (1950) and Kramer and Kozlowski (1960) discuss the relationship among photosynthesis, respiration, carbohydrate storage, growth and distribution of assimilate in trees. In general, current photosynthate not used in respiration is either used in the elaboration of new protoplasm or stored as starch. Kozlowski and Winget (1964) reported that most of the reserve food used in shoot elongation of red pine came from old needles. Larson (1964) observed that red pine seedlings made better height growth when previous year, rather than current year, needles were left unshaded.

Bourdeau (1958c) investigated the relationship between growth and unit rate of photosynthesis in seedlings of several coniferous species and suggested the use of a $\frac{P+R}{R}$ (P = net photosynthesis, R = dark respiration) ratio for the rapid screening of nursery stock for individuals likely to exhibit rapid growth. Wassink and Richardson (1951) studied the relationship between shoot illumination and root growth in sycamore maple and northern red oak. They found that for sycamore maple rate of root growth was related directly to rate of photosynthesis, but that northern red oak did not rely on currently produced photosynthate for root growth.

Ladell (1963) found a relationship between needle density and tracheid length in Scotch pine. Ovington (1962) discusses the relation-

ship between photosynthesis and growth in woodland ecosystems. Thut and Loomis (1944) point out that net photosynthesis determines the dry matter content of plant tissue but that growth depends to a considerable extent on hydration and other factors. It has been suggested that the photosynthetic process is a direct participant in the photoperiodic reaction of cocklebur (Bonner and Liverman 1953). Watson (1947), reporting on the variation in net assimilation rate of field crops between species and varieties, stated that increment dry matter in any interval of time is the integral of the product of net assimilation rate and leaf area; and that leaf area may be regarded as the integrated measure of all complexities of growth and differentiation other than the assimilatory process.

MATERIAL AND METHOD

Seed Acquisition

Seed was acquired in 1963 from eight European sources (Table 1). The seed was supplied by governmental agencies and a private seed dealer. For all seed lots, origin was certified by the agency or dealer, and information descriptive of the place of origin supplied. All seed was stand collected. Seed sources were chosen to sample the north-south European range of Scotch pine, to minimize longitudinal distribution and to lie in Eastern Europe, where natural stands are most frequently encountered. Because Scotch pine does not occur naturally at lower elevations in the Southern portion of its range, it was impossible to obtain seed lots of identical elevational origin.

Table 1. Seed origin

ISU Number	Country	Locality	North Latitude	East Longitude	Elevation meters
211	Finland	Kivalo	66°	26°	150
210	Finland	Vilppula	62°	24°	100
208	Finland	Hango	60°	23°	15
217	Latvia	Lernburg	57°	25°	100
216	Poland	Olsztyn	54°	20°	137
214	Czechoslovakia	Habry	50°	16°	780
215	Czechoslovakia	Presov	49°	21°	690
218	Bulgaria	Rhodopes	42°	25°	1,220

Study I

Seed from the eight seed sources was sown in 1-gallon pots in the greenhouse in a randomized complete block design on November 24, 1964. From the time of sowing until the seedlings were removed from the greenhouse, they were exposed to a 16-hour photoperiod, obtained by lengthening natural daylight with incandescent lamps. The light intensity supplied by the lamps was 40 foot-candles at pot height. The soil in which the seed was sown was a 1:1:1 mixture of acid peat, sand and Clarion loam. After germination the seedlings were thinned to two per pot.

Height was measured twice (May 25, 1965 and July 8, 1965) during the growth period. At the time of the first height measurement, the seedlings were thinned to one per pot by severing stems at the soil line. From the seedling tops thus removed, three of each seed source were drawn at random and fresh and dry weights obtained for the entire top, juvenile needles (strap-shaped needles appearing first and borne singly), mature needles (needles borne two to a fascicle appearing in the axils of juvenile needles) and the stem.

After all seedlings had set bud in late July, they were divided into three experimental groups of adjacent, eight-seedling blocks. One group, consisting of two blocks, was used for equipment testing. The first group of six blocks (group I) was used to determine the effect of seed source on rates of photosynthesis and respiration at one light intensity (6,000 foot-candles). The second group of six blocks (group II) was used to determine the effect of seed source and light intensity on

rates of photosynthesis and respiration. The two light intensities used were 3,000 and 9,000 foot-candles, and a split-plot experimental design was employed, with adjacent blocks combined to make the main units to which the two intensities were randomly applied.

Rates of net photosynthesis were measured in the laboratory by enclosing each seedling in a controlled-environment chamber (described in Broerman, et al., 1966), exposing it to the appropriate light intensity for a 10-minute preconditioning period and then monitoring the change in carbon dioxide concentration within the closed system with an infrared gas analyzer. The pot was enclosed in a 3-mil polythylene bag sealed around the base of the stem to isolate CO_2 evolved in soil respiration from the measurement system. The output signal from the gas analyzer was recorded on a strip-chart, and a tangent to the curve thus generated was drawn at the point where the curve crossed the chart line indicating a carbon dioxide concentration of 400 ppm. From this tangent the rate of consumption or evolution of carbon dioxide in ppm per hour was computed, and these rates were converted to rates in mg CO_2 per hour, per seedling and per gram fresh and dry weight of needles, by a computer program. Rates of dark respiration were measured by darkening the chamber with light-tight cloth immediately after measuring rate of net photosynthesis and proceeding as above. Rates of gross photosynthesis were obtained by adding rates of net photosynthesis and dark respiration. Chamber temperature was maintained at $15 \pm 1^{o}C$ for all measurements.

After rates of photosynthesis and respiration were measured, all seedlings were immediately harvested, and height and fresh and dry

weights of the top, stem, juvenile needles, mature needles and roots were recorded. Dry weights were obtained by drying the fresh material for 24 hours in a 70°C oven.

For both experiments, one block or main unit was moved from the greenhouse to the laboratory during one day so that greenhouse blocks became time blocks for the rate measurements. Preliminary testing showed no effect of time of day, during daylight, on rates of photosynthesis and respiration. All laboratory measurements for the two experiments were made within a 12-day period.

Study II

On the basis of preliminary experiments three seed sources exhibiting good growth were selected from the original eight. These were 208, a northern source, 216, a low altitude central European source, and 214, a higher altitude central European source. Seedlings from the three sources were started in the greenhouse on the same date in late fall, moved to the nursery the following summer, and returned to the greenhouse in the fall, where they were grown until rates of photosynthesis and respiration were measured early in the summer of the second year. While in the greenhouse, a constant 16-hour photoperiod was maintained as in Study I. At the time of measurement, all seedlings had completed a second flush of height growth. These seedlings were used in experiments (1) to determine the effect of seed source, light intensity, needle temperature, and CO_2 concentration on rates of photosynthesis and respiration, and (2) to determine the effect of seed source, high

light intensity, and temperature on CO_2 compensation point and time to reach CO_2 compensation point. A three-replicated, randomized complete block design with a factorial arrangement of treatments was used in the first experiment. As previously, greenhouse blocks were transformed into blocks in time for laboratory measurements. Light intensities of 3,000, 6,000 and 9,000 foot-candles, chamber temperatures of 5° and 15° and CO_2 concentrations of 400, 300, and 200 ppm were used. Needle temperatures were measured potentiometrically with copper-constantin thermocouples.

Each seedling of a specified treatment combination was sealed in a controlled-environment chamber having a CO_2 concentration of approximately 450 ppm, exposed to the appropriate temperature and light intensity, and left in the chamber until CO_2 concentration ceased to decrease. Before being placed in the chamber, the pot containing the seedling was watered, allowed to drain, sealed in a polyethylene bag, and the entire seedling weighed. When the CO_2 concentration decreased to the point of no detectable change over a 10-minute period, the chamber was darkened and CO_2 evolution recorded for a 20-minute period. The seedling was then removed from the chamber, weighed and harvested. Height and fresh and dry weights of stem, top, needles and roots were recorded. From the recorded curves of CO_2 depletion, rates of net photosynthesis were determined by drawing tangent lines at each of the three CO_2 concentrations and proceeding as in Study I. From the recorded curve of CO_2 evolution in the dark, rate of dark respiration was computed by using the change in CO_2 concentration during the second 10 minutes

of the 20-minute dark period. Gross photosynthesis was computed by adding rates of net photosynthesis and dark respiration.

Analyses of variance and planned comparisons were carried out for each photosynthesis variable at each of the three CO_2 concentrations; for respiration, CO_2 compensation point, and time elapsed to CO_2 compensation point; and for the height and weight data.

Two subsequent experiments were carried out using similar seedlings of the same three seed sources to determine the effect of lower light intensities and seed source on rates of photosynthesis and respiration. Light intensities of 50, 350, and 650 foot-candles and 1,200, 1,800, and 2,400 foot-candles were employed. Short-time rates of net photosynthesis and dark respiration at a CO_2 concentration of 400 ppm were measured as in Study I. Analyses of variance and planned comparisons were carried out on all dependent variables according to the randomized complete block designs employed.

RESULTS

Study I: Growth and Distribution of Assimilate

Effect of seed source

Growth varied significantly among the eight seed sources (Figure 1). Most growth variables showed a curvilinear relationship with latitude of seed source, with growth maxima occurring at latitudes between 47^{o} and 51^{o}[1].

Height Height measured during and at the end of the growth period showed a curvilinear relationship with latitude of seed source. The latitude of calculated maximum height obtained by differentiating the second-degree polynomial of best fit, was 50^{o} (Figure 2).

Fresh and dry weight Fresh and dry weights of seedlings and of seedling tops, mature needles and total needles exhibited a curvilinear relationship with latitude of seed source (Figures 3 and 4). Fresh and dry weights of stems and roots were strongly related to latitude of seed source, but the quadratic component of the latitude of seed source sum of squares was not consistently significant at the one percent probability level (Table 2). Fresh and dry weights of juvenile needles were related linearly to latitude of seed source, but were less variable than fresh and dry weights of mature needles (Figure 5, Table 2). The intermediate sample of seedling tops, taken during the growth period, in-

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[1]All latitudes presented are north latitudes.

Figure 1. One replication of the eight seed sources just before harvest. (Top, left to right, 66^{o}, 62^{o}, 60^{o}, 57^{o}; Bottom, left to right, 54^{o}, 49^{o}, 50^{o}, 42^{o}).

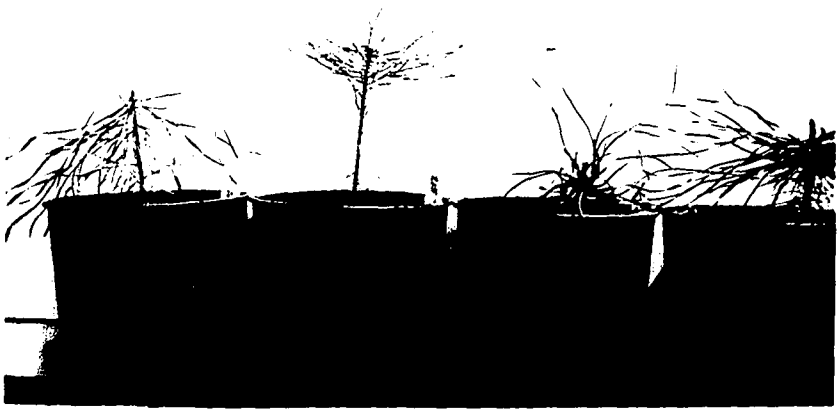


Figure 2. The relationship between height and latitude of seed source for three measurement dates.

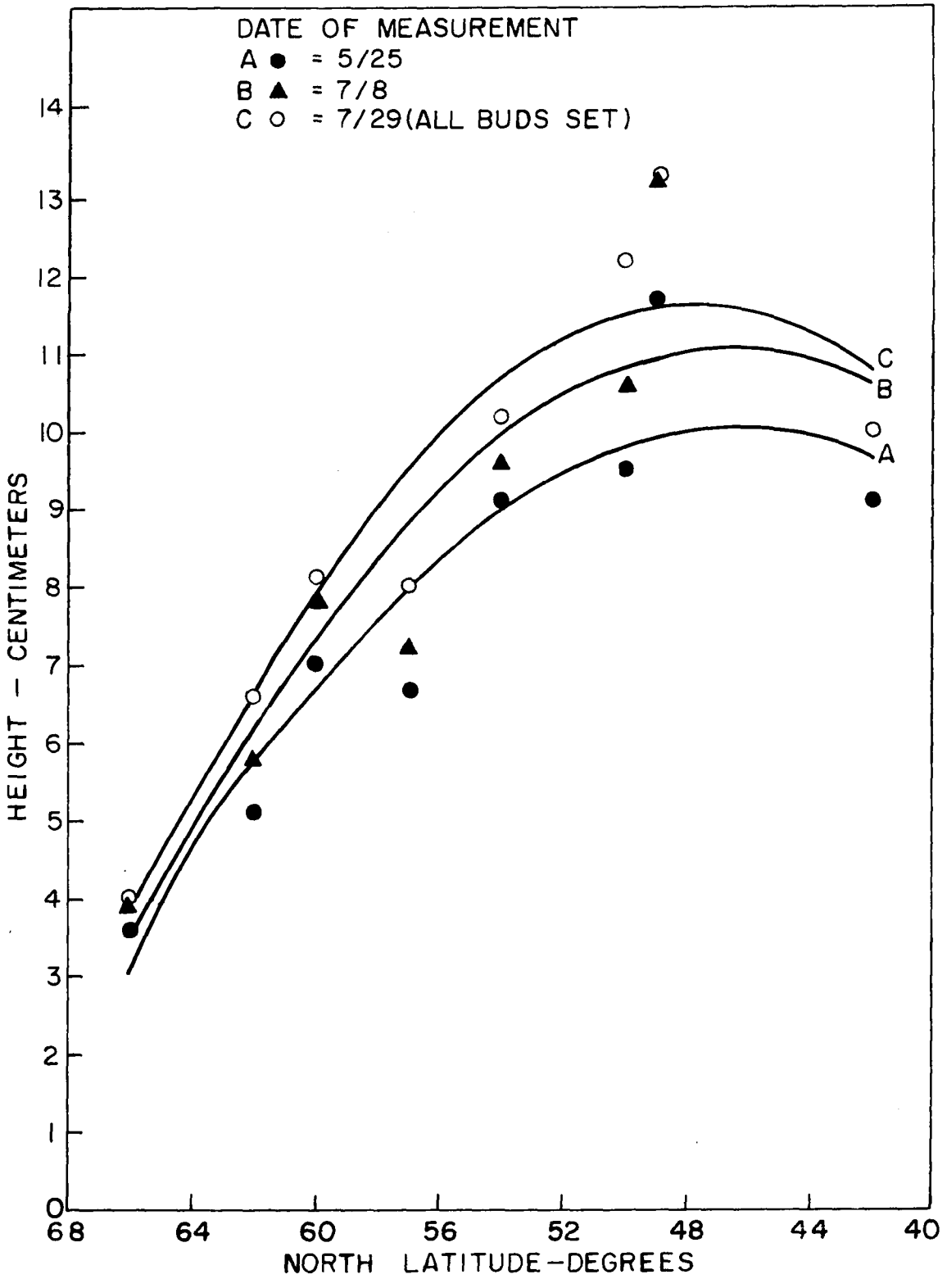

DATE OF MEASUREMENT
A ● = 5/25
B ▲ = 7/8
C ○ = 7/29(ALL BUDS SET)
HEIGHT - CENTIMETERS
NORTH LATITUDE-DEGREES
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
68
64
60
56
52
48
44
40
A
B
C

Figure 3. The relationship between fresh weight and latitude of seed source.

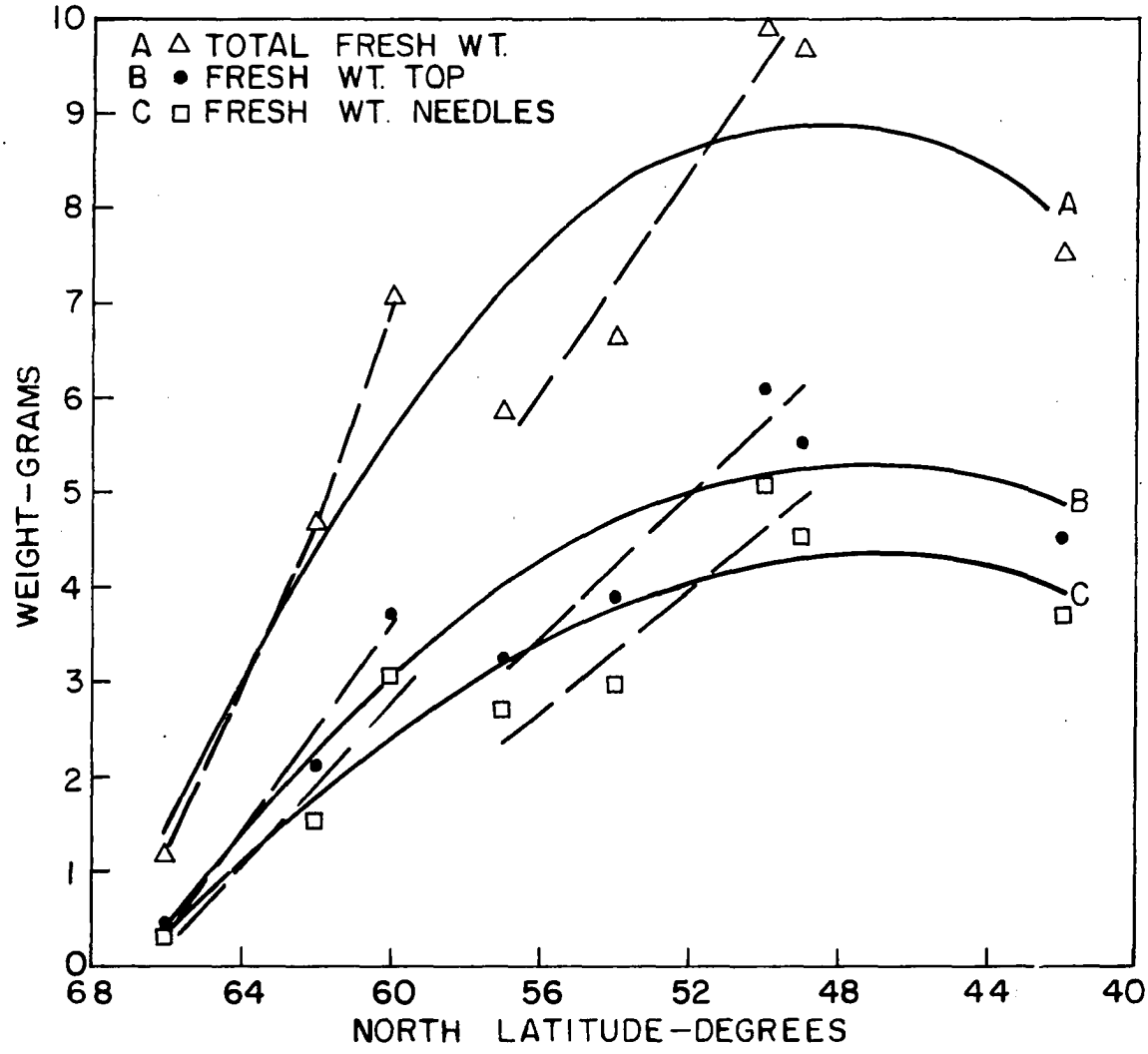

A △ TOTAL FRESH WT.
B • FRESH WT. TOP
C □ FRESH WT. NEEDLES
WEIGHT-GRAMS
NORTH LATITUDE-DEGREES
0
1
2
3
4
5
6
7
8
9
10
68
64
60
56
52
48
44
40
A
B
C

Figure 4. The relationship between dry weight and latitude of seed source.

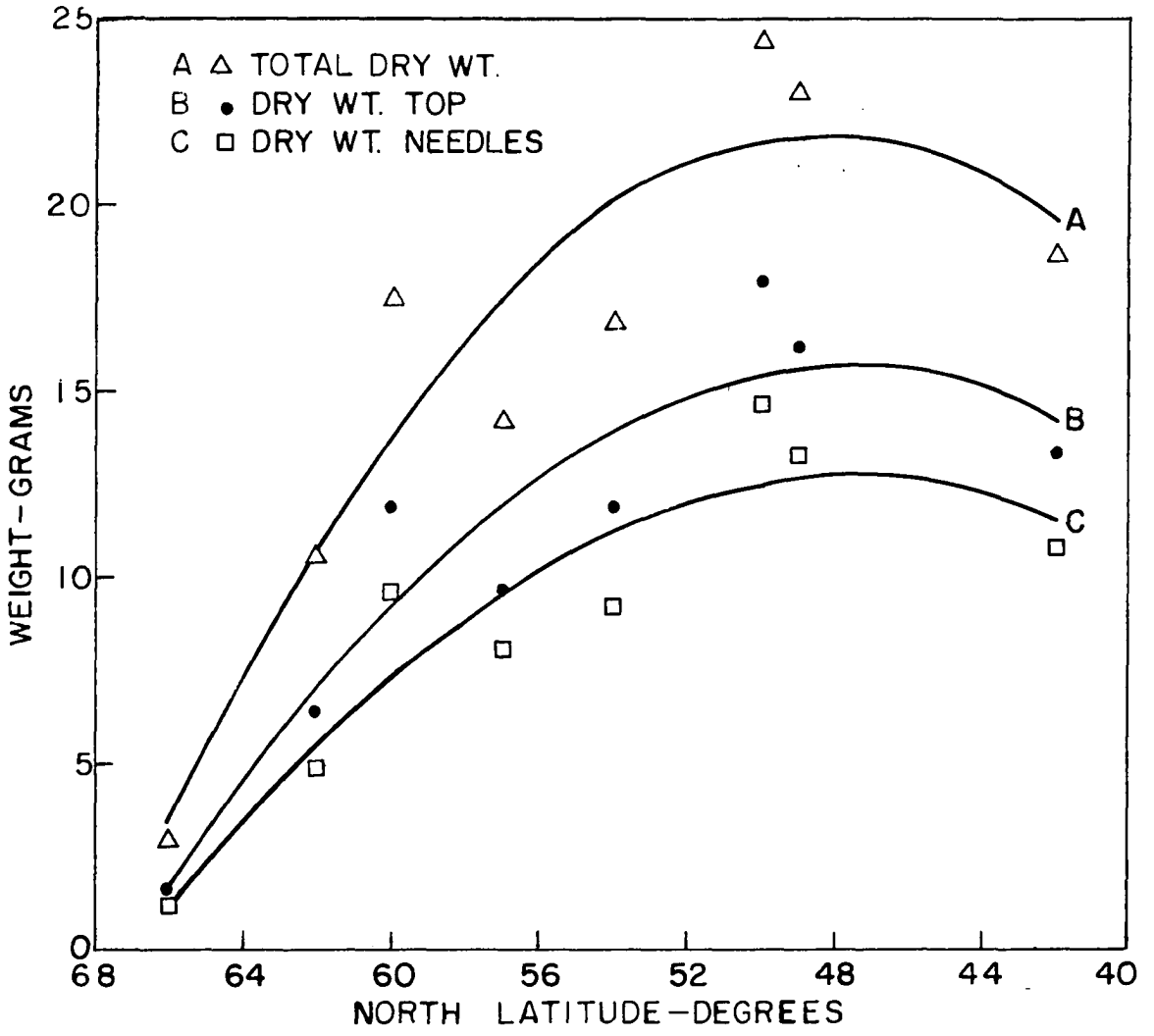

A △ TOTAL DRY WT.
B • DRY WT. TOP
C □ DRY WT. NEEDLES
A
B
C
25
20
15
10
5
0
WEIGHT-GRAMS
68
64
60
56
52
48
44
40
NORTH LATITUDE-DEGREES

Figure 5. The relationship between fresh weight of juvenile and mature needles, and latitude of seed source.

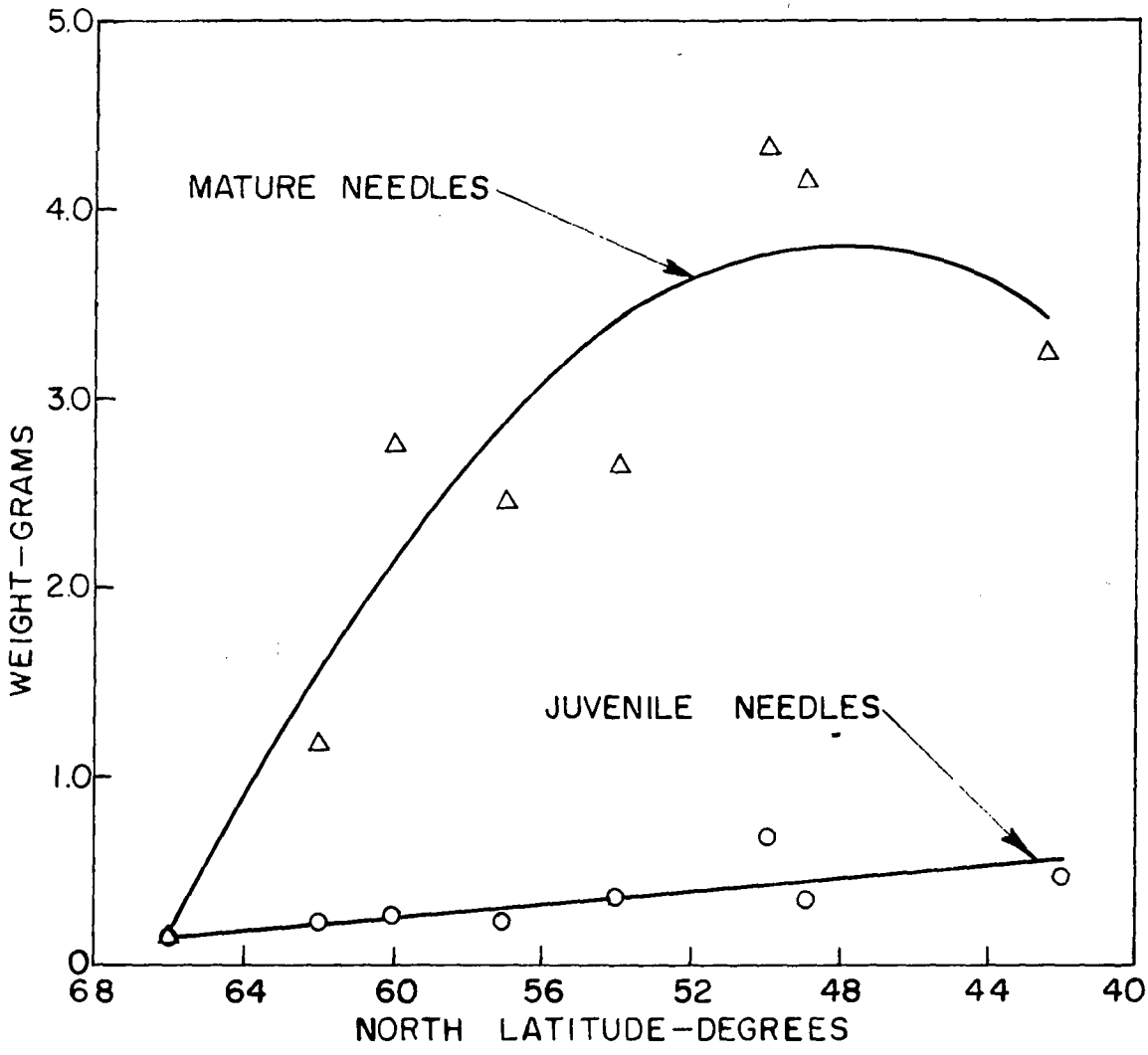

5.0
4.0
3.0
2.0
1.0
0
WEIGHT—GRAMS
MATURE NEEDLES
JUVENILE NEEDLES
68
64
60
56
52
48
44
40
NORTH LATITUDE—DEGREES

Table 2. Mean squares from analyses of variance for fresh and dry weight data

Dependent variable	Source of Variation					
	Replication	Seed source				Error
		total	(linear)	(quadratic)	(lack of fit)	
	5 d.f.[a]	7 d.f.	(1 d.f.)	(1 d.f.)	(5 d.f.)	35 d.f.
Fresh wt. top	2.59	19.74**	92.60**	28.60**	3.42	2.98
Fresh wt. stem	0.17	0.60*	2.64**	1.01*	0.11	0.16
Fresh wt. juvenile needles	0.11	0.18**	0.65**	0.02**	0.11	0.08
Fresh wt. mature needles	1.52	11.36**	51.60**	17.80**	2.03	1.75
Fresh wt. total needles	1.53	13.69**	64.05**	19.05**	2.56	2.01
Fresh wt. roots	3.72	6.69*	21.20**	13.62**	2.40	2.10
Fresh wt. total	12.05	47.83*	202.20**	82.80**	10.16	9.48
Dry wt. top	0.24	1.65**	7.49**	2.58**	0.30	0.23
Dry wt. stem	0.01	0.05*	0.23**	0.09*	0.01	0.01
Dry wt. juvenile needles	0.01	0.01**	0.07**	0.01**	0.01	0.01
Dry wt. mature needles	0.13	0.93**	4.00**	1.49**	0.20	0.14
Dry wt. total needles	0.14	1.14**	5.11**	1.76**	0.22	0.16
Dry wt. roots	0.11	0.17	0.60**	0.39**	0.04	0.05
Dry wt. total	0.65	2.84	12.32**	4.98**	0.52	0.48

[a] d.f. = degrees of freedom.

* Significant at the 5% probability level.

** Significant at the 1% probability level.

dicated that the latitudinal pattern of needle, stem and top weights was established at least two months before the final measurements were taken (Table 3). Maxima for all weight variables exhibiting a curvilinear relationship with latitude of seed source occurred between 47° and 50° (Figures 3 and 4).

Shoot-root ratios Shoot-root ratios, based on mean fresh and dry weights of tops and roots, varied in a curvilinear fashion with latitude of seed source (Figure 6). No estimate of error was possible because shoot-root ratios for individual seedlings were not computed. A second degree polynomial relating shoot-root ratio to latitude of seed source accounted for approximately 90 percent of variation in mean shoot-root ratios.

Percent distribution of assimilate Percents of total dry weight found in different portions of the seedlings are presented in Table 4. Percent of total dry weight in the needles increased with decreasing latitude of seed source, and percent of total dry weight in the roots decreased with decreasing latitude of seed source.

Non-latitudinal variations Departures from the curvilinear or linear relationship with latitude of seed source exhibited by growth variables were small but perhaps biologically significant. Two major discontinuities were apparent; the first between the three sources originating north of the Baltic (66°, 62°, 60°) and the central European sources (57°, 54°, 50°, 49°), and the second between the central European sources and the single southern European source (42°) (dashed lines, Figure 3).

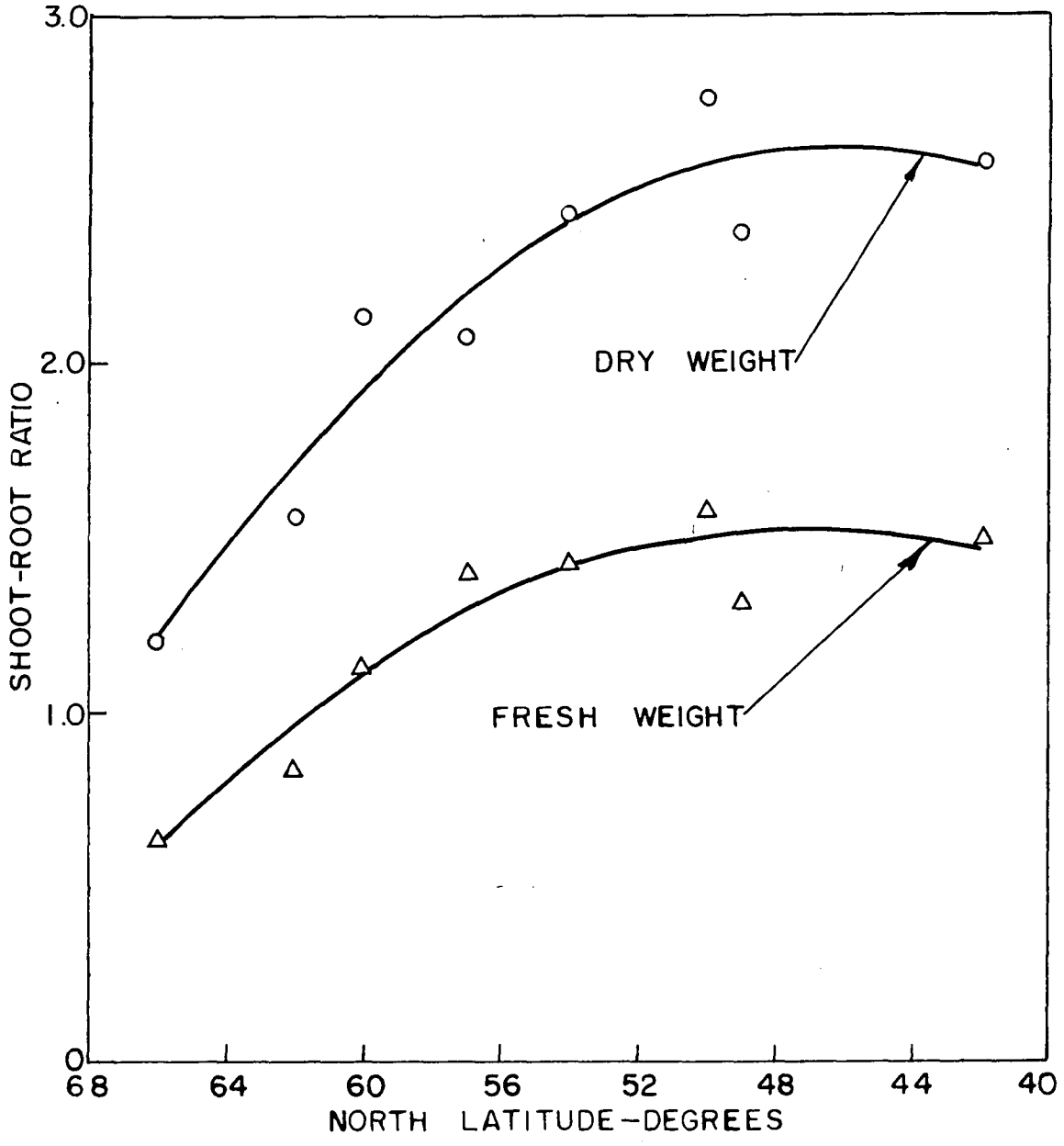
Table 3. Mean fresh and dry weights from the intermediate sample of seedling tops

Seed source	Fresh weight					Dry weight				
	Top	Stem	Juvenile needles	Mature needles	Total needles	Top	Stem	Juvenile needles	Mature needles	Total needles
	g	g	g	g	g	g	g	g	g	g
66°(211)	0.30	0.03	0.13	0.14	0.27	0.11	0.01	0.05	0.05	0.10
62°(210)	0.68	0.07	0.12	0.49	0.61	0.23	0.03	0.04	0.16	0.20
60°(208)	1.16	0.15	0.17	0.84	1.01	0.40	0.08	0.05	0.27	0.32
57°(217)	1.01	0.12	0.18	0.71	0.89	0.28	0.04	0.06	0.18	0.24
54°(216)	1.30	0.28	0.35	0.67	1.02	0.39	0.10	0.11	0.18	0.29
50°(214)	1.46	0.42	0.48	0.56	1.04	0.40	0.13	0.16	0.11	0.27
49°(215)	1.84	0.43	0.42	0.99	1.41	0.54	0.15	0.14	0.25	0.39
42°(218)	1.50	0.44	0.38	0.68	1.06	0.45	0.13	0.16	0.16	0.32

Table 4. Percent distribution of assimilate (dry weight)

Seedling part	Seed source							
	66°(211)	62°(210)	60°(208)	57°(217)	54°(216)	50°(214)	49°(215)	42°(218)
Top	55.2	61.0	68.1	67.5	71.0	73.4	70.4	72.1
Needles	41.4	45.6	54.9	56.4	54.1	59.9	57.9	58.1
Stem	13.8	15.4	13.2	11.1	16.9	13.5	12.5	14.0
Roots	44.8	39.0	31.9	32.5	29.0	26.6	29.6	27.9

Figure 6. The relationship between shoot-root ratio and latitude of seed source.


3.0
2.0
1.0
0
SHOOT-ROOT RATIO
DRY WEIGHT
FRESH WEIGHT
68
64
60
56
52
48
44
40
NORTH LATITUDE-DEGREES

Study I: Rates of Photosynthesis and Respiration

Effect of seed source

Rates of net and gross photosynthesis, expressed on a per seedling basis, varied in a curvilinear fashion with latitude of seed source, and maximum rates occurred at approximately 50^{o}. Rates of net and gross photosynthesis expressed per gram fresh or dry weight of needles also varied in a curvilinear fashion with latitude of seed source. However, maximum rates occurred in seedlings of the northernmost seed source, which grew least. Minimum rates occurred at approximately 50^{o}, the latitude at which total needle weights were maximum (Figures 7 and 8, Table 5).

Discontinuities in the relationship between net and gross photosynthesis per seedling and latitude of seed source occurred at the same latitudes as the discontinuities that occurred in the relationships between growth variables and latitude of seed source (dashed lines, Figure 7). These discontinuities did not appear, however, when rates of photosynthesis per gram of fresh or dry needle weight were plotted over latitude.

No significant differences occurred in rates of respiration among seed sources, but addition of rates of respiration to rates of net photosynthesis strengthened the relationship between latitude of seed source and rates of (gross) photosynthesis (Table 5). Rates of respiration were at or just under threshold values for accurate short-time detection by the measurement system; therefore, instrumental error may be partially responsible for the great variability in observed rates.

Table 5. Mean squares from analyses of variance for photosynthesis and respiration data

Dependent variable	Source of Variation					
	Replication	Seed source				Error
		total	(linear)	(quadratic)	(lack of fit)	
	5 d.f.[a]	7 d.f.	(1 d.f.)	(1 d.f.)	(5 d.f.)	35 d.f.
Net photosynthesis/ seedling	34.6	60.4*	142.1**	109.7*	35.6	20.9
Net photosynthesis/ g fresh wt.	11.1	140.0**	450.0**	365.0**	33.0	13.0
Net photosynthesis/ g dry wt.	116.5	1,162.3**	3,772.8**	3,083.1**	213.4	136.3
Respiration/seedling	30.2	11.9	0.3	4.9	15.6	6.7
Respiration/g fresh wt.	13.5	3.8	14.1	3.4	1.9	4.2
Respiration/g dry wt.	123.3	32.5	118.9	46.3	12.5	38.5
Gross photosynthesis/ seedling	75.2	109.4**	129.0*	161.0*	95.2	31.4
Gross photosynthesis/ g fresh wt.	47.1	176.4**	622.0**	434.1**	35.7	27.2
Gross photosynthesis/ g dry wt.	468.1	1,470.2**	5,231.3**	3,884.9**	235.1	263.5

[a] d.f. = degrees of freedom.

* Significant at the 5% probability level.

** Significant at the 1% probability level.

Figure 7. The relationship between rate of gross photosynthesis per seedling and per gram fresh and dry weight of needles, and latitude of seed source.

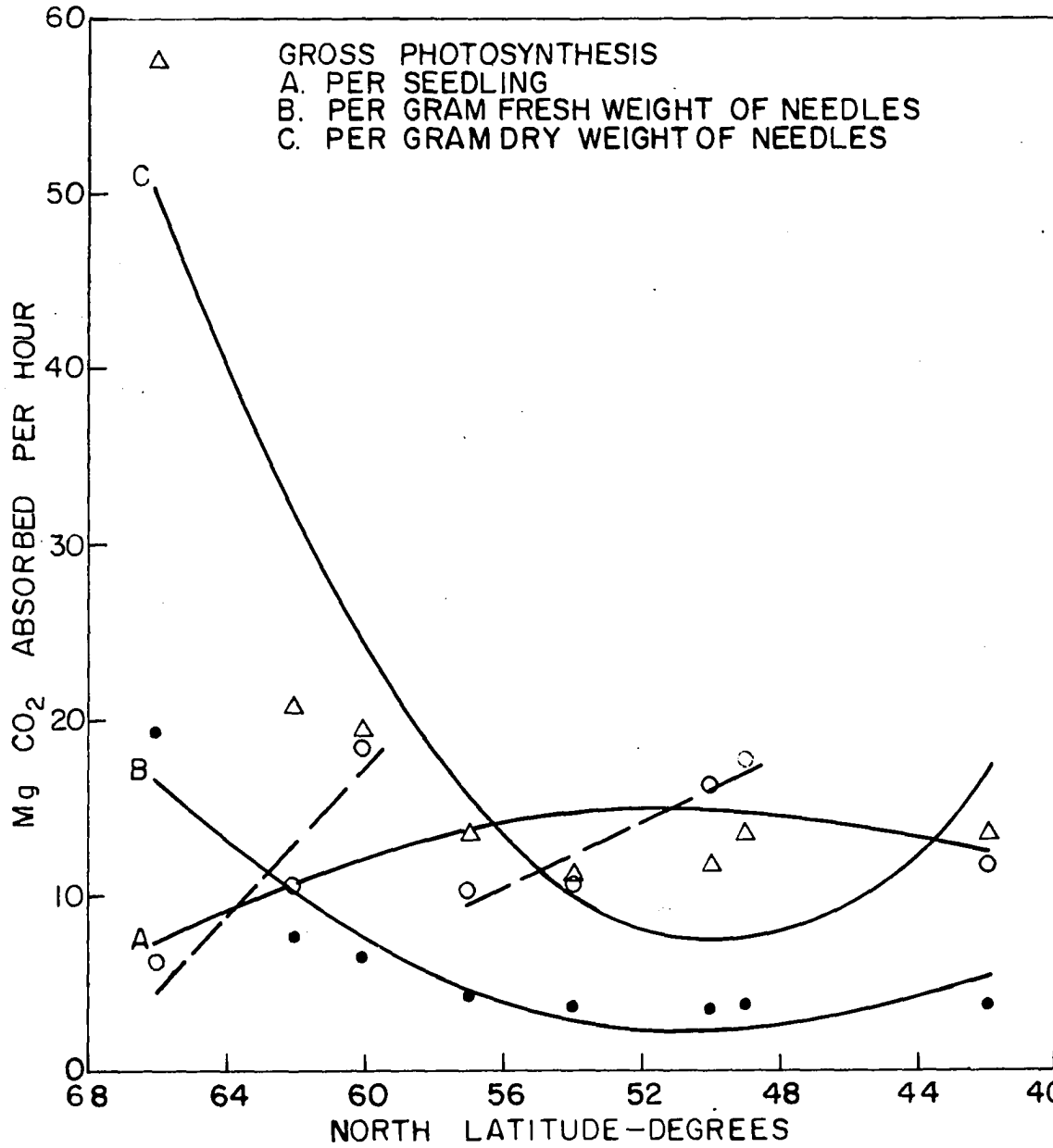
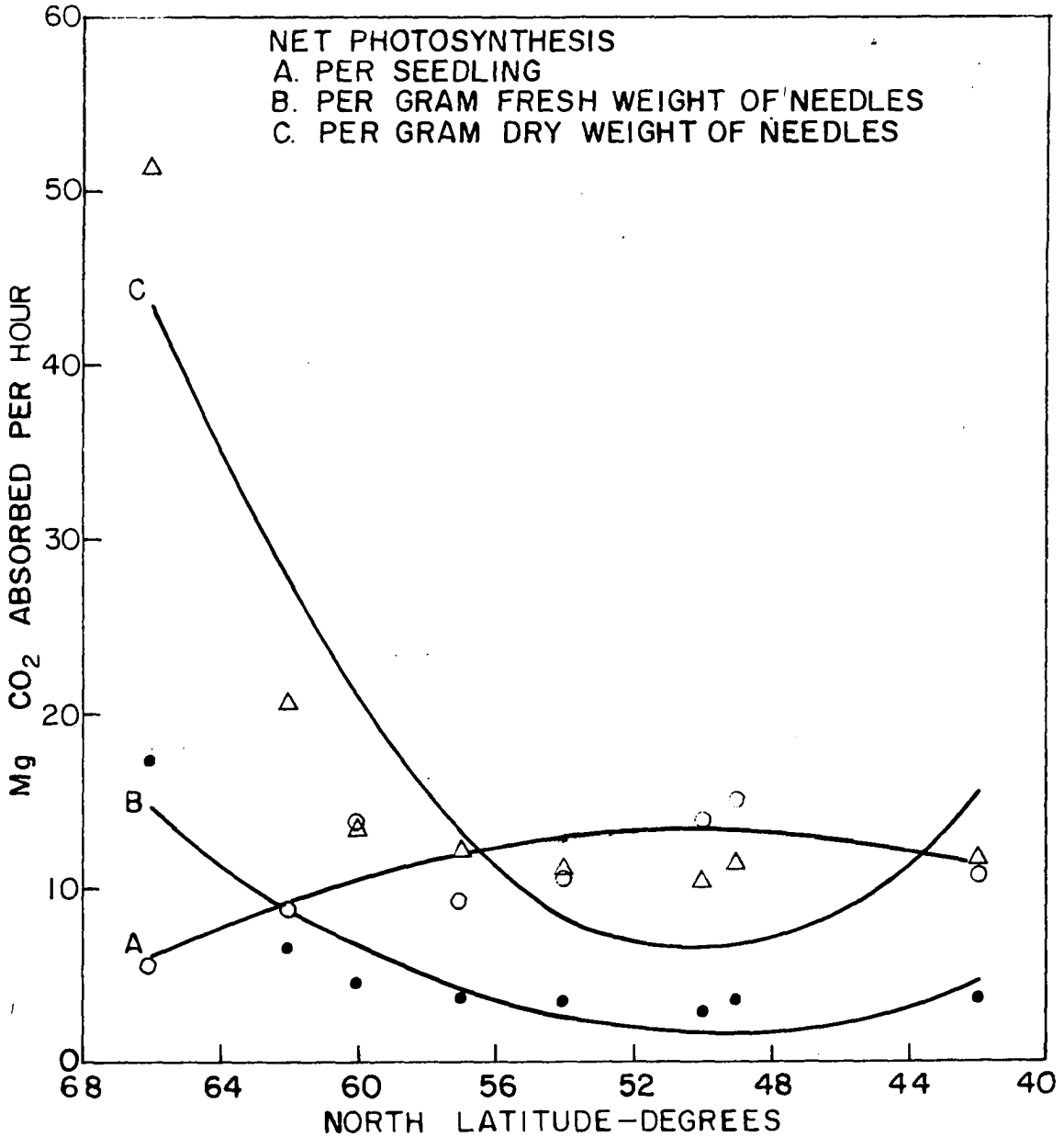

GROSS PHOTOSYNTHESIS
A. PER SEEDLING
B. PER GRAM FRESH WEIGHT OF NEEDLES
C. PER GRAM DRY WEIGHT OF NEEDLES
Mg CO_2 ABSORBED PER HOUR
NORTH LATITUDE—DEGREES
60
50
40
30
20
10
0
68
64
60
56
52
48
44
40
A
B
C

Figure 8. The relationship between rate of net photosynthesis per seedling and per gram fresh and dry weight of needles, and latitude of seed source.


NET PHOTOSYNTHESIS
A. PER SEEDLING
B. PER GRAM FRESH WEIGHT OF NEEDLES
C. PER GRAM DRY WEIGHT OF NEEDLES
Mg CO2 ABSORBED PER HOUR
0
10
20
30
40
50
60
68
64
60
56
52
48
44
40
NORTH LATITUDE—DEGREES
A
B
C

Effect of light intensity

Light intensity and latitude of seed source had an interacting effect on rate of net photosynthesis when expressed per gram of needle dry weight (Table 6). The northernmost seed source (66^{o}) exhibited a decrease in rate of net photosynthesis over the 3,000 to 9,000 foot-candle range, while the next seed source south (62^{o}) exhibited an increase in rate of net photosynthesis over the same light intensity range (Figure 9). When rates of photosynthesis measured at 6,000 foot-candles were plotted with the rates at 3,000 and 9,000 foot-candles for all seed sources, the greatest variation in rate of photosynthesis was again exhibited by the two northernmost sources (Figure 10).

Table 6. Mean squares from analyses of variance for photosynthesis and respiration data, group II

Dependent variable	Source of variation					
	Replication	Light intensity	Error a	Seed source	Seed source X light int.	Error b
	2 d.f.[a]	1 d.f.	2 d.f.	7 d.f.	7 d.f.	28 d.f.
Net Ps/ seedling	27.3	13.7	41.9	95.5**	41.6	28.8
Net Ps/g fresh wt.	0.3	11.7	8.4	30.1**	2.2	2.7
Net Ps/g dry wt.	18.7	57.0	34.9	114.0**	42.0*	17.8

[a] d.f. = degrees of freedom

* Significant at the 5% probability level

** Significant at the 1% probability level

Figure 9. The relationship between rate of net photosynthesis per gram dry weight of needles and latitude of seed source, for light intensities of 3,000 and 9,000 foot-candles.

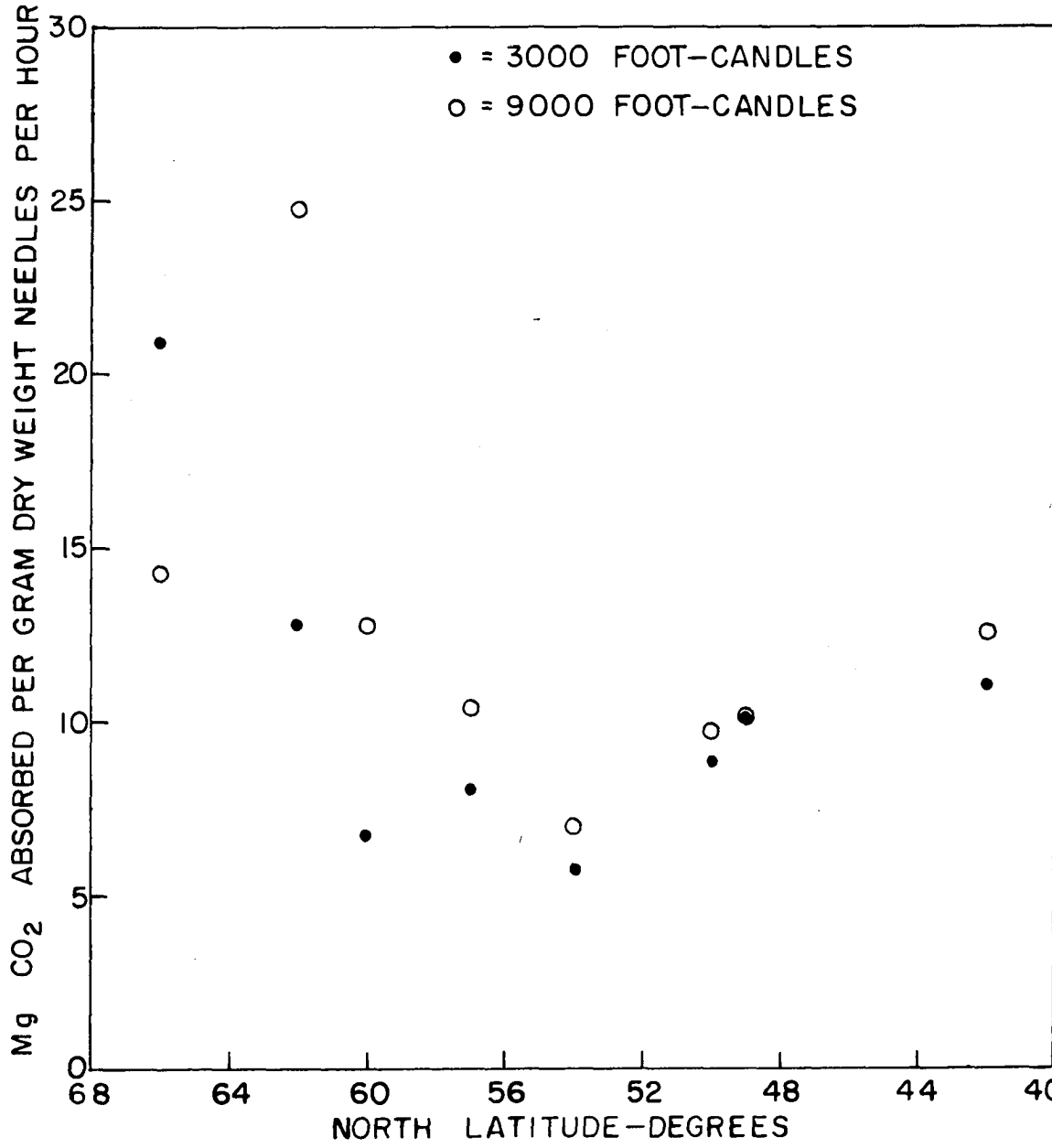
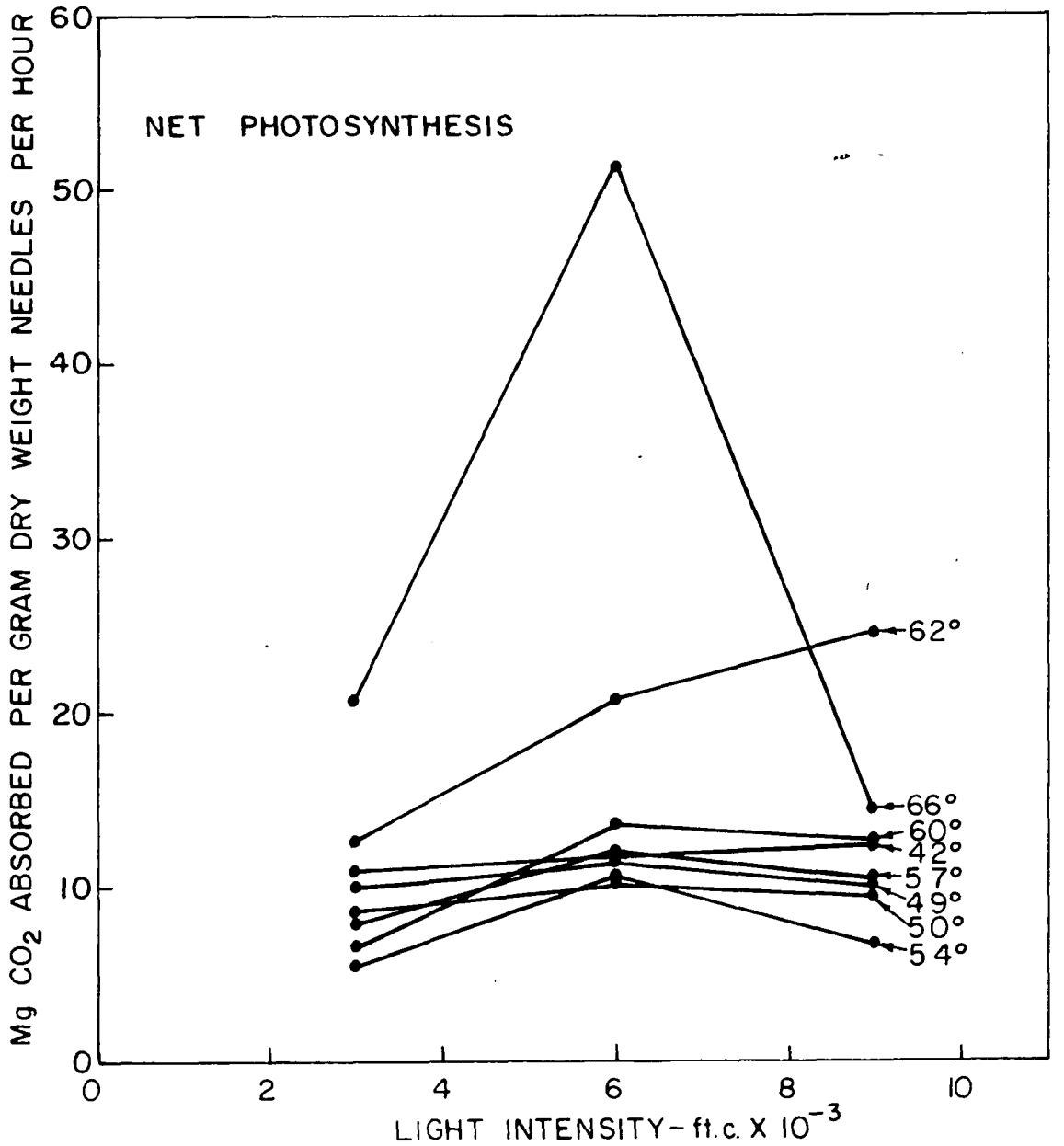

• = 3000 FOOT-CANDLES
o = 9000 FOOT-CANDLES
Mg CO_2 ABSORBED PER GRAM DRY WEIGHT NEEDLES PER HOUR
0
5
10
15
20
25
30
68
64
60
56
52
48
44
40
NORTH LATITUDE-DEGREES

Figure 10. The relationship of rate of net photosynthesis per gram dry weight of needles to light intensity, for the eight seed sources.


NET PHOTOSYNTHESIS
Mg CO_2 ABSORBED PER GRAM DRY WEIGHT NEEDLES PER HOUR
LIGHT INTENSITY - ft.c. X 10^{-3}
0
10
20
30
40
50
60
0
2
4
6
8
10
62°
66°
60°
42°
57°
49°
50°
54°

Study II: Growth and Distribution of Assimilate

Effect of seed source

Growth data for second-year seedlings were taken in three experiments, each corresponding to an experiment in which rates of photosynthesis were measured. In all three experiments, seed was sown on the same day, and the seedlings were grown in the same environment. Inasmuch as results of the three experiments were similar, only the results of the first study are presented.

Height, fresh and dry weights of top, stem, needles, roots and total seedlings were greater for the seed sources from 54° and 50° than for the seed source from 60° (Table 7). The seed source from 54° produced slightly more total dry weight than the seed source from 50°, with the difference occurring mainly in the needles. Mean values of the other growth variables were consistently, but not significantly, greater for the seed source from 54° than for the seed source from 50° (Table 8). Apparently in seedlings older than one year, the latitudinal growth pattern exhibited in the first year was retained, but the growth maxima were shifted north. Shoot-root ratios were similar for all three seed sources, but in the seed source from 54°, a greater percent of total dry weight occurred in the needles.

Regression analyses between growth variables and latitude of seed source were not carried out; therefore latitudes of maximum growth could not be calculated.

Table 7. Mean squares from analyses of variance for growth variables

Dependent variable	Replication	Seed Source			Error
		total	$(C_1)^a$	$(C_2)^b$	
	1 d.f.[c]	2 d.f.	(1 d.f.)	(1 d.f.)	32 d.f.
Height	50.17	112.69	180.50**	48.16	36.58
Fresh wt. top	208.80	544.66**	665.40**	423.36**	54.65
Fresh wt. stem	17.33	63.92**	122.62**	5.42**	6.55
Fresh wt. needles	106.16	275.77*	217.57**	333.02**	30.44
Fresh wt. roots	322.20	548.06*	940.04**	157.29	154.75
Fresh wt. total	2,673.58	1,453.48*	2,450.00**	456.30	368.79
Dry wt. top	9.98	68.54**	78.88**	58.41**	8.96
Dry wt. stem	2.72	6.74**	12.80*	0.65**	0.85
Dry wt. needles	2.28	37.37*	27.83**	46.70**	5.52
Dry wt. roots	55.18	25.32*	50.60**	0.03	6.65
Dry wt. total	112.29	158.37*	256.28**	60.67	24.01

[a] C_1 = Comparison 1; 208(60°) vs mean of 216(54°) and 214(50°).

[b] C_2 = Comparison 2; 216(54°) vs 214(50°).

[c] d.f. = degrees of freedom.

* Significant at the 5% probability level.

** Significant at the 1% probability level.

Table 8. Means for growth variables

Dependent variable	units	Seed Source 208(60°)	216(54°)	214(50°)
Height	cm.	16.2	22.4	19.5
Fresh wt. top	g	18.20	31.52	23.12
Fresh wt. stem	g	4.42	8.81	7.86
Fresh wt. needles	g	13.77	22.71	15.26
Fresh wt. roots	g	20.61	34.01	28.89
Fresh wt. total	g	43.67	65.53	56.81
Dry wt. top	g	6.81	11.51	8.39
Dry wt. stem	g	1.86	3.29	2.96
Dry wt. needles	g	4.96	8.22	5.43
Dry wt. roots	g	5.04	7.59	7.52
Dry wt. total	g	11.85	19.10	15.92

Study II: Photosynthesis and Respiration

Rates of photosynthesis and respiration were measured in three experiments. The randomized complete block experiment employing a factorial arrangement of temperature, light intensity and seed source treatments showed no significant interactions among these three independent variables in their effects on rates of photosynthesis, respiration, and CO_2 compensation point. Interactions between CO_2 concentration and the other three independent variables were obviously present but were statistically untestable because analyses of variance were carried out within each of three CO_2 concentrations. The two other randomized complete block experiments, which employed light intensities of 1,200, 1,800 and 2,400 foot-candles and 50, 350 and 650 foot-candles, showed no interacting effects of seed source and light intensity on rates of photosynthesis or respiration.

Rates of gross photosynthesis (sum of rates of dark respiration and rates of net photosynthesis) are subject to possible error from two sources; dark respiration may not correspond to light respiration, and, in the experiment employing temperature as a treatment, needle temperatures were lower in the dark than in the light.

Effect of seed source

Seed source had no effect on the magnitude of CO_2 compensation point or time to reach CO_2 compensation point (Tables 9 and 11). At a CO_2 concentration of 400 ppm, seed source had no effect on rates of net or gross photosynthesis, but at a CO_2 concentration of 300 ppm, rate

Table 9. Mean CO_2 compensation points and time to reach CO_2 compensation point by seed source

Seed source	CO_2 compensation point	Time to reach CO_2 compensation point
	ppm	minutes
60°(208)	161	154
54°(216)	141	122
50°(214)	148	144

of gross photosynthesis per seedling was less in the northernmost (60°) seed source than the mean of the two central European sources (54° and 50°). At the 200 ppm CO_2 concentration, rates of net and gross photosynthesis per seedling were greater in the seed source from 54° than in either of the other two seed sources (Tables 10 and 11). No differences due to seed source occurred in rates of photosynthesis per gram of fresh or dry needle weight in the experiment with light intensities of 3,000, 6,000 and 9,000 foot-candles (Table 11). In the experiment with light intensities of 1,200, 1,800 and 2,400 foot-candles, rate of gross photosynthesis per seedling of the seed source from 54° was greater than the rate of the seed source from 50°. Rates for both the 50° and 60° sources were less than the rates for the 54° source (Tables 12 and 13). In the experiment with light intensities of 50, 350 and 650 foot-candles, rates of photosynthesis per seedling in the two central European sources (54° and 50°) were greater than in the northernmost (60°) seed source (Tables

Table 10. Mean rates of net and gross photosynthesis and respiration for each of three CO_2 concentrations, for the three seed sources (light intensities of 3,000, 6,000 and 9,000 foot-candles pooled)

Dependent variable	CO_2 Concentration	Seed source		
		60°(208)	54°(216)	50°(214)
	ppm	Mg CO_2 absorbed or evolved per hour		
Net photosynthesis/seedling	400	35.0	41.6	34.1
	300	23.3	32.0	25.2
	200	9.5	14.0	8.2
Net photosynthesis/g fresh wt.	400	2.6	2.9	2.1
	300	1.5	2.3	1.6
	200	0.5	1.0	0.5
Net photosynthesis/g dry wt.	400	7.4	5.5	6.3
	300	4.4	4.2	4.8
	200	1.6	1.8	1.6
Respiration/seedling	---	14.5	19.0	17.2
Respiration/g fresh wt.	---	1.2	1.2	1.1
Respiration/g dry wt.	---	3.4	2.6	3.3
Gross photosynthesis/seedling	400	49.5	60.6	51.3
	300	37.8	51.1	42.5
	200	24.0	33.0	25.4
Gross photosynthesis/g fresh wt.	400	3.8	4.2	3.1
	300	2.7	3.6	2.6
	200	1.8	2.3	1.6
Gross photosynthesis/g dry wt.	400	10.8	8.1	9.7
	300	7.8	6.8	8.2
	200	5.0	4.4	4.9

Table 11. Mean squares from analyses of variance for water loss, photosynthesis and respi including light intensity, temperature, CO_2 and seed source treatments

Dependent variable		Replication	Light intensity			Temper-ature		See
			Total	(linear)	(lack of fit)		Total	$(C_1)^b$
		1 d.f.[a]	2 d.f.	(1 d.f.)	(1 d.f.)	1 d.f.	2 d.f.	(1 d.f.
CO_2 compensation point		173.0	6,146*	11,882**	411	15,088**	1,256	NS
Time to reach CO_2 compensation point		4.0	157	NS	NS	17,778**	3,374	NS
Water loss		230.0	46.4	NS	NS	600.2*	76.4	NS
Net Ps/seedling	400 ppm	409.32	341.15*	NS	NS	1,848.85*	201.43	NS
Net Ps/seedling	300 ppm	10.79	368.51*	689.72*	47.66	92.64	252.83	NS
Net Ps/seedling	200 ppm	0.57	152.90	305.28*	0.49	162.56	109.89	NS
Net Ps/g fresh wt.	400 ppm	1.68	2.35	NS	NS	22.58*	2.22	NS
Net Ps/g fresh wt.	300 ppm	0.43	3.24	NS	NS	3.37	2.54	NS
Net Ps/g fresh wt.	200 ppm	0.24	0.95	NS	NS	0.11	1.06	NS
Net Ps/g dry wt.	400 ppm	0.03	3.21*	NS	NS	72.56**	10.59	NS
Net Ps/g dry wt.	300 ppm	2.30	10.69*	13.21**	8.17*	1.26*	1.11	NS
Net Ps/g dry wt.	200 ppm	0.09	3.90*	7.51**	0.28	6.88*	0.18	NS
Rs/seedling		83.94	17.39	NS	NS	213.21**	61.05*	102.9
Rs/g fresh wt.		0.32	0.07	NS	NS	3.91**	0.11	NS
Rs/g dry wt.		0.06	0.26	NS	NS	13.99**	2.44	NS
Gross Ps/seedling	400 ppm	864.16	493.96*	NS	NS	3,317.38**	425.55*	NS
Gross Ps/seedling	300 ppm	154.96	534.48*	1,030.92**	37.98	587.01*	540.42*	102.9
Gross Ps/seedling	200 ppm	70.76	271.99*	544.01**	0.001	3.45	278.93*	216.2
Gross Ps/g fresh wt.	400 ppm	3.47	3.03	NS	NS	45.29**	3.30	NS
Gross Ps/g fresh wt.	300 ppm	1.50	3.76	NS	NS	14.53*	3.35	NS
Gross Ps/g fresh wt.	200 ppm	1.11	1.08	NS	NS	2.68	1.67	NS
Gross Ps/g dry wt.	400 ppm	0.18	4.28	NS	NS	150.51**	22.06	NS
Gross Ps/g dry wt.	300 ppm	1.63	10.49	NS	NS	23.75*	5.84	NS
Gross Ps/g dry wt.	200 ppm	0.003	3.00	NS	NS	1.27	1.35	NS

[a] d.f. = degrees of freedom

[b] C_1 = comparison 1, 208(60°) vs. mean of 216(54°) and 214(50°)

[c] C_2 = comparison 2, 216(54°) vs. 214(50°)

* Significant at the 5% probability level

** Significant at the 1% probability level

loss, photosynthesis and respiration variables for the experiment
seed source treatments

ty ck of fit) d.f.)	Temper-ature 1 d.f.	Total 2 d.f.	Seed source (C_1)[b] (1 d.f.)	(C_2)[c] (1 d.f.)	Light Int.X Temp. 2 d.f.	Light Int.X Seed source 4 d.f.	Temp.X Seed source 2 d.f.	Light Int.XTemp.X Seed source 4 d.f.	Error 17 d.f.
411	15,088**	1,256	NS	NS	3,457	1,764	3,570	885	1,302
NS	17,778**	3,374	NS	NS	804	407	1,915	749	901
NS	600.2*	76.4	NS	NS	23.6	197.4	28.1	121.7	88.4
NS	1,848.85*	201.43	NS	NS	76.64	365.11	206.25	116.69	279.93
47.66	92.64	252.83	NS	NS	146.20	81.17	361.10	60.15	92.30
0.49	162.56	109.89	NS	NS	60.46	28.16	54.62	30.96	44.66
NS	22.58*	2.22	NS	NS	4.18	2.39	2.35	2.42	3.21
NS	3.37	2.54	NS	NS	4.52	1.20	3.31	1.91	2.00
NS	0.11	1.06	NS	NS	1.24	0.53	0.63	0.66	0.50
NS	72.56**	10.59	NS	NS	2.75	2.19	2.80	1.07	5.91
8.17*	1.26*	1.11	NS	NS	0.78	1.37	2.18	2.56	1.46
0.28	6.88*	0.18	NS	NS	0.81	0.41	0.72	0.86	0.55
NS	213.21**	61.05*	102.90**	19.20	15.25	21.40	33.72	15.90	10.45
NS	3.91**	0.11	NS	NS	0.85	0.40	0.37	0.46	0.26
NS	13.99**	2.44	NS	NS	1.16	2.18	2.20	1.10	1.20
NS	3,317.38**	425.55*	NS	NS	148.88	333.95	405.41	186.58	356.09
37.98	587.01*	540.42*	102.90**	19.20*	127.15	77.36	615.28	59.76	125.00
0.001	3.45	278.93*	216.24	341.65*	127.97	9.62	173.80	33.27	64.16
NS	45.29**	3.30	NS	NS	8.65	3.35	4.34	4.64	5.02
NS	14.53*	3.35	NS	NS	8.80	1.74	4.73	3.46	3.38
NS	2.68	1.67	NS	NS	3.93	1.10	1.38	1.67	1.25
NS	150.51**	22.06	NS	NS	7.38	2.01	9.88	3.81	10.07
NS	23.75*	5.84	NS	NS	1.27	1.12	2.33	3.69	3.67
NS	1.27	1.35	NS	NS	2.64	1.05	0.86	1.71	1.44

nd 214(50°)

Table 12. Mean rates of net and gross photosynthesis and respiration for the three seed sources (light intensities of 1,200, 1,800 and 2,400 foot-candles pooled)

Dependent variable	Seed source		
	60°(208)	54°(216)	50°(214)
	Mg CO_2 absorbed or evolved per hour		
Net photosynthesis/seedling	35.2	52.5	32.6
Net photosynthesis/g fresh wt.	3.6	2.9	3.7
Net photosynthesis/g dry wt.	10.4	8.3	10.8
Respiration/seedling	8.0	9.7	6.5
Respiration/g fresh wt.	0.8	0.5	0.7
Respiration/g dry wt.	2.4	1.4	2.1
Gross photosynthesis/ seedling	43.2	62.2	39.2
Gross photosynthesis/g fresh wt.	4.5	3.4	4.4
Gross photosynthesis/g dry wt.	12.8	9.8	12.9

Table 13. Mean squares from analyses of variance for photosynthesis and respiration data intensities of 1,200, 1,800 and 2,400 foot-candles

Dependent variable	Source of variation: Replication	Light intensity			
		Total	(linear)	(lack of fit)	
	2 d.f.[a]	2 d.f.	(1 d.f.)	(1 d.f.)	2 d
Net photosynthesis/seedling	111.95	361.44	NS	NS	1,049
Net photosynthesis/g fresh wt.	0.75	0.76	NS	NS	1
Net photosynthesis/g dry wt.	11.88	4.41	NS	NS	16
Respiration/seedling	1.06	83.49**	166.90**	0.09*	23
Respiration/g fresh wt.	0.01	0.37**	0.50**	0.25*	0
Respiration/g dry wt.	0.29	6.06*	4.41**	1.65	4
Gross photosynthesis/seedling	123.58	772.67	NS	NS	1,364
Gross photosynthesis/g fresh wt.	0.97	1.89	NS	NS	3
Gross photosynthesis/g dry wt.	15.83	12.82	NS	NS	29

[a] d.f. = degrees of freedom

[b] C_1 = comparison 1, 208(60^o) vs. mean of 216(54^o) and 214(50^o)

[c] C_2 = comparison 2, 216(54^o) vs. 214(50^o)

* Significant at the probability level of 5%

** Significant at the probability level of 1%

ata

iance for photosynthesis and respiration data for the experiment with light
,400 foot-candles

.on

on	Source of variation							
	Light intensity			Seed source				Error
Tot	Total	(linear)	(lack of fit)	Total	$(C_1)^b$	$(C_2)^c$	L.I.X.	
2 d	2 d.f.	(1 d.f.)	(1 d.f.)	2 d.f.	(1 d.f.)	(1 d.f.)	S.S.	16 d.f.
049	361.44	NS	NS	1,049.51	NS	NS	133.13	351.59
1	0.76	NS	NS	1.64	NS	NS	1.16	1.42
16	4.41	NS	NS	16.27	NS	NS	10.69	14.28
23	83.49**	166.90**	0.09	23.08**	NS	NS	5.56	13.37
0	0.37**	0.50**	0.25*	0.28**	0.33*	0.24*	0.08	0.05
4	6.06*	4.41**	1.65	4.41*	2.27*	2.14	.70	.52
364	772.67	NS	NS	1,364.98*	343.38	2,370.16*	176.09	464.56
3	1.89	NS	NS	3.14	NS	NS	1.55	1.73
29	12.82	NS	NS	29.37	NS	NS	14.24	18.03

ı of 216(54°) and 214(50°)

50°)

5%

of 1%

14 and 15).

Table 14. Mean rates of net and gross photosynthesis and respiration for the three seed sources (light intensities of 50, 350, and 650 foot-candles pooled)

Dependent variable	Seed source 60^{o}(208)	54^{o}(216)	50^{o}(214)
	Mg. CO_2 absorbed or evolved per hour		
Net photosynthesis/seedling	7.0	13.3	13.5
Net photosynthesis/gm. fresh wt.	0.8	0.5	0.6
Net photosynthesis/gm. dry wt.	2.0	1.5	1.8
Respiration/seedling	1.1	4.5	2.9
Respiration/gm. fresh wt.	0.1	0.2	0.1
Respiration/gm. dry wt.	0.3	0.5	0.4
Gross photosynthesis/seedling	8.1	17.8	16.3
Gross photosynthesis/gm. fresh wt.	0.9	0.7	0.7
Gross photosynthesis/gm. dry wt.	2.3	2.0	2.2

The experiment with light intensities of 3,000, 6,000 and 9,000 foot-candles showed a lower rate of respiration per seedling in the northernmost source than in the two central European sources, but, in this experiment, no differences among seed sources in rate of respiration per gram fresh or dry weight of needles occurred (Tables 10 and 11). The experiment with light intensities of 1,200, 1,800 and 2,400 foot-candles showed rate of respiration per gram fresh weight of needles to be greater in the northernmost source than in the two central European sources. Rate of respiration per gram fresh weight of needles was greater in the seed source from 50^{o} than in the one from 54^{o} (Tables 12 and 13). The experiment with the lowest light intensities (50, 350 and 650 foot-

Table 15. Mean squares from analyses of variance for photosynthesis and respiration light intensities of 50, 350 and 650 foot-candles

Dependent variable	Source of varia			
	Replication	Light intensity		
		Total	(linear)	(lack of fit)
	2 d.f.[a]	2 d.f.	(1 d.f.)	(1 d.f.)
Net photosynthesis/seedling	11.91	415.99**	803.20**	29.83
Net photosynthesis/g fresh wt.	0.12	1.03**	2.02**	0.01
Net photosynthesis/g dry wt.	0.48	8.90**	17.64**	0.10
Respiration/seedling	26.46	18.14*	22.98*	14.17
Respiration/g fresh wt.	0.14	0.02	NS	NS
Respiration/g dry wt.	0.88	0.14	NS	NS
Gross photosynthesis/seedling	71.88	589.49**	1,095.12**	83.03
Gross photosynthesis/g fresh wt.	0.51	1.27**	2.46**	0.04
Gross photosynthesis/g dry wt.	2.54	11.04**	21.98**	0.11

[a] d.f. = degrees of freedom

[b] C_1 = comparison 1, 208(60°) vs. mean of 216(54°) and 214(50°)

[c] C_2 = comparison 2, 216(54°) vs. 214(50°)

* Significant at the 5% probability level

** Significant at the 1% probability level

for photosynthesis and respiration data for the experiment with
ot-candles

Source of variation								
	Light intensity			Seed source				Error
otal	(linear)	(lack of fit)	Total	$(C_1)^b$	$(C_2)^c$	L.I.X S.S.	
d.f.	(1 d.f.)	(1 d.f.)	2 d.f.	(1 d.f.)	(1 d.f.)	4 d.f.	16 d.f.
15.99**	803.20**	29.83	123.19**	246.14**	0.10	40.60	14.92
1.03**	2.02**	0.01	0.17	NS	NS	0.02	0.07
8.90**	17.64**	0.10	0.55	NS	NS	0.19	0.63
18.14*	22.98*	14.17	25.38**	38.86**	11.96	6.76	3.83
0.02	NS	NS	0.002	NS	NS	0.02	0.01
0.14	NS	NS	0.05	NS	NS	0.19	0.10
39.49**	1,095.12**	83.03	245.24**	481.15**	9.72	73.49	27.93
1.27**	2.46**	0.04	0.15	NS	NS	0.05	0.13
11.04**	21.98**	0.11	0.25	NS	NS	0.53	1.05

216(54°) and 214(50°)

candles) showed rate of respiration per seedling to be greater in the two central European sources than in the northernmost source (Tables 14 and 15).

Effect of light intensity

CO_2 compensation point decreased as light intensity increased over the 3,000 to 9,000 foot-candle range (Figure 11). However, light intensity over this range had no effect on time to reach CO_2 compensation point and no effect on total water loss during the measurement period (Table 11).

At a CO_2 concentration of 400 ppm, light intensity over the 3,000 to 9,000 foot-candle range had no significant effect on rates of net or gross photosynthesis. However, at a CO_2 concentration of 300 ppm, rate of net photosynthesis per seedling and per gram dry weight of needles, and rate of gross photosynthesis per seedling, increased with light intensity. At a 200 ppm CO_2 concentration, rate of net photosynthesis per seedling and per gram dry weight of needles increased with light intensity, as did rate of gross photosynthesis per seedling. However, rates of gross photosynthesis per gram fresh or dry weight of needles were little affected by light intensity at this CO_2 concentration (Figures 12 and 13, Table 11). Over the 1,200 to 2,400 foot-candle range, at a CO_2 concentration of 400 ppm, light intensity had no effect on rates of net or gross photosynthesis (Table 13), but at the same CO_2 concentration, rates of net and gross photosynthesis increased with light intensities over the 50 to 650 foot-candle range (Figure 14, Table 15). These results indicate that at a CO_2 concentration of 400 ppm, light saturation occurred between 650 and 1,200 foot-candles.

Rate of dark respiration per seedling increased linearly with preceding light intensity over the 50 to 650 foot-candle range (Table 15).

Figure 11. The relationship between CO_2 compensation point and light intensity.

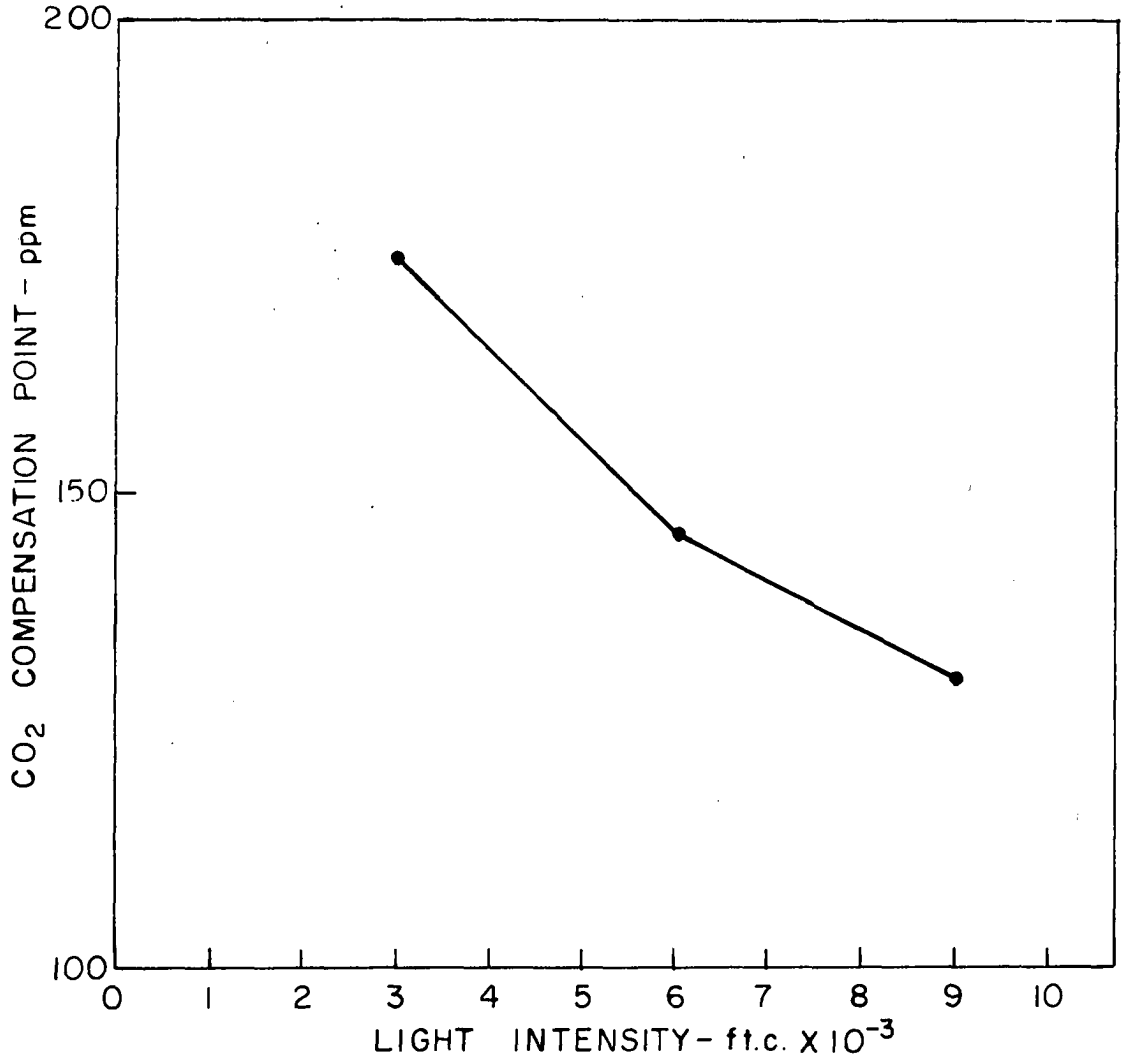

200
150
100
CO_2 COMPENSATION POINT - ppm
0
1
2
3
4
5
6
7
8
9
10
LIGHT INTENSITY - ft.c. X 10^{-3}

Figure 12. The relationship between rate of net and gross photosynthesis per seedling and light intensity, for three CO_2 concentrations (400, 300, and 200 ppm).

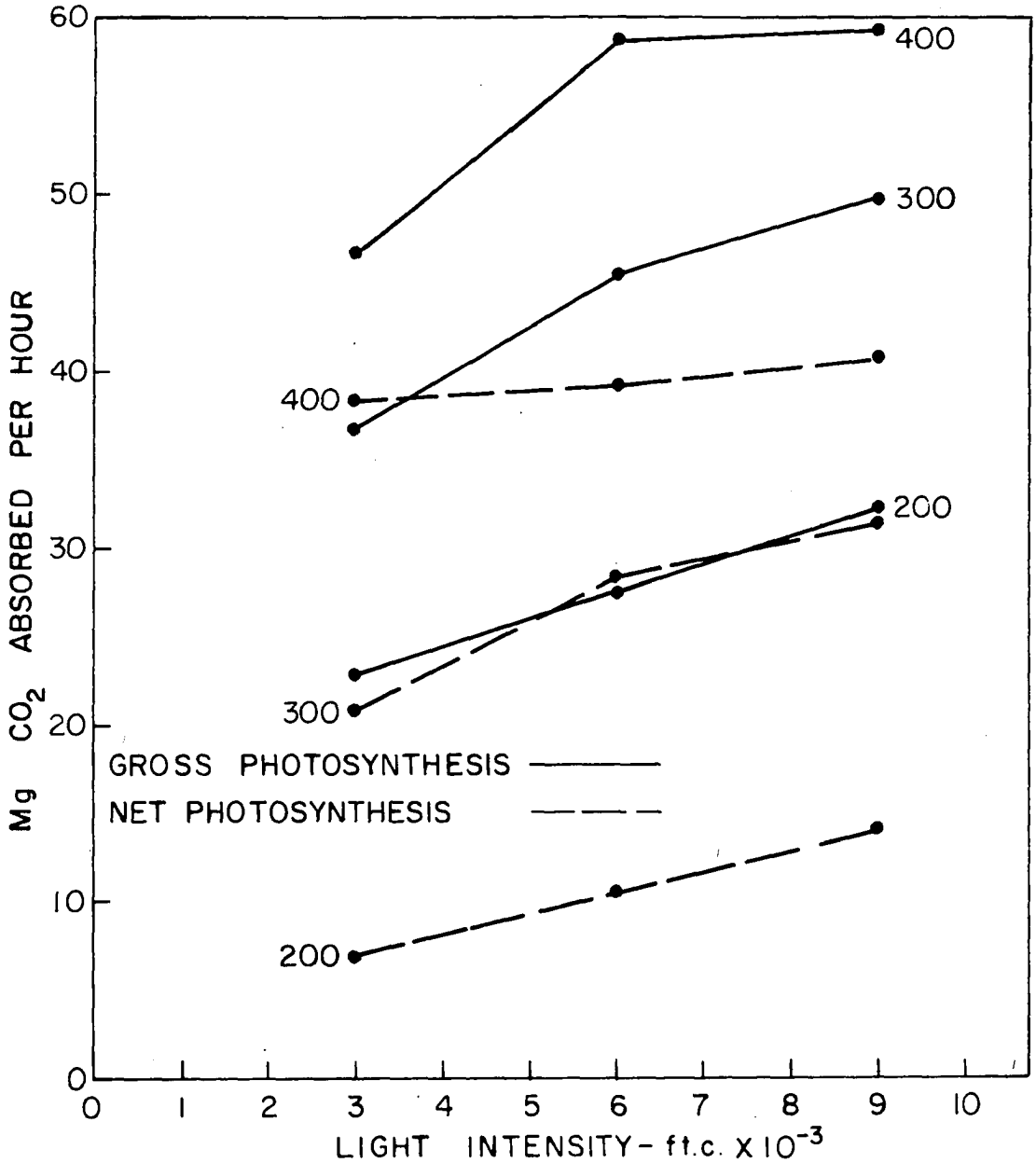

60
50
40
30
20
10
0
Mg CO_2 ABSORBED PER HOUR
400
300
400
200
300
GROSS PHOTOSYNTHESIS
NET PHOTOSYNTHESIS
200
0 1 2 3 4 5 6 7 8 9 10
LIGHT INTENSITY - ft.c. X 10^{-3}

Figure 13. The relationship between rate of net photosynthesis per gram fresh and dry weight of needles and light intensity, for three CO_2 concentrations (400, 300 and 200 ppm).

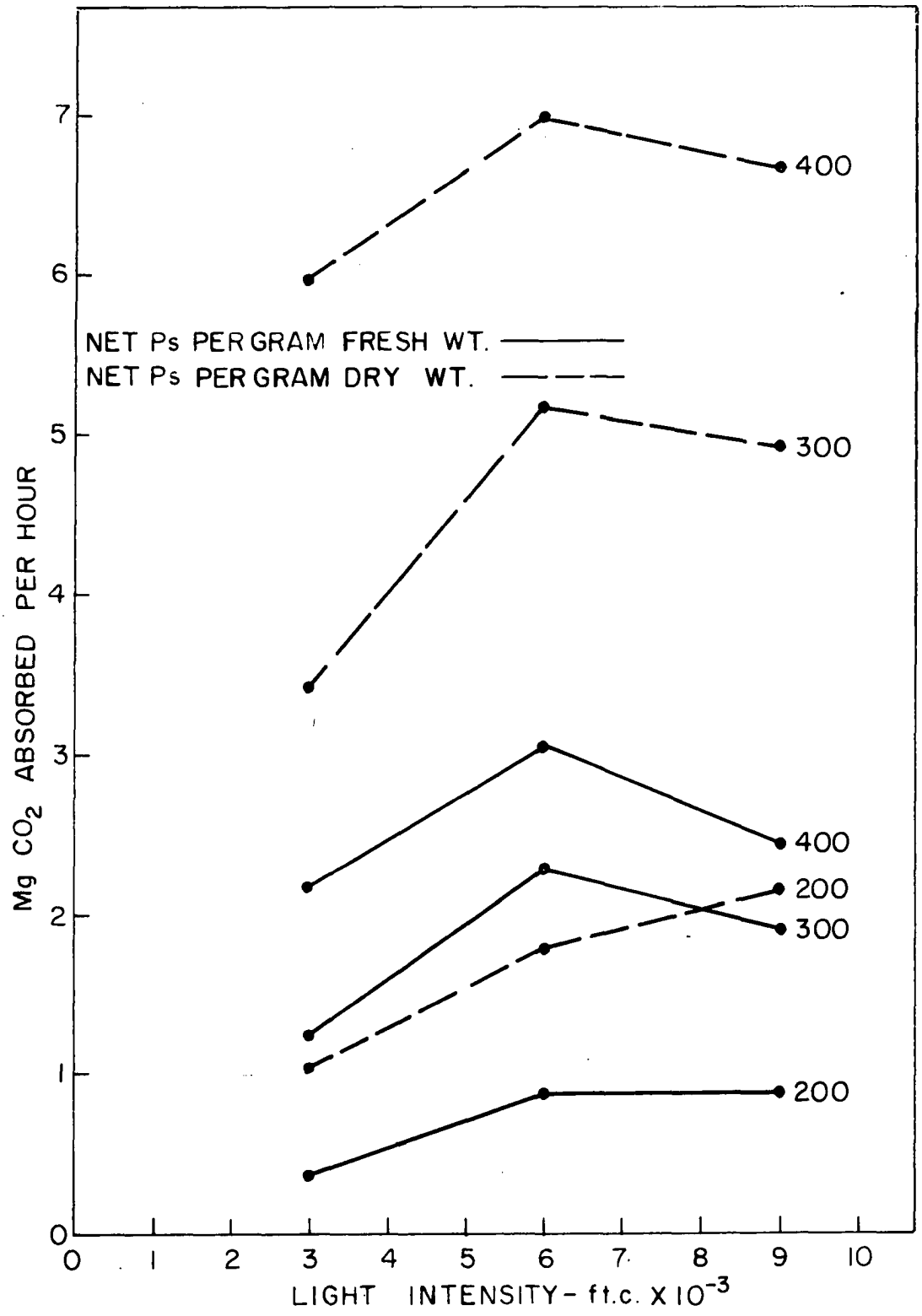
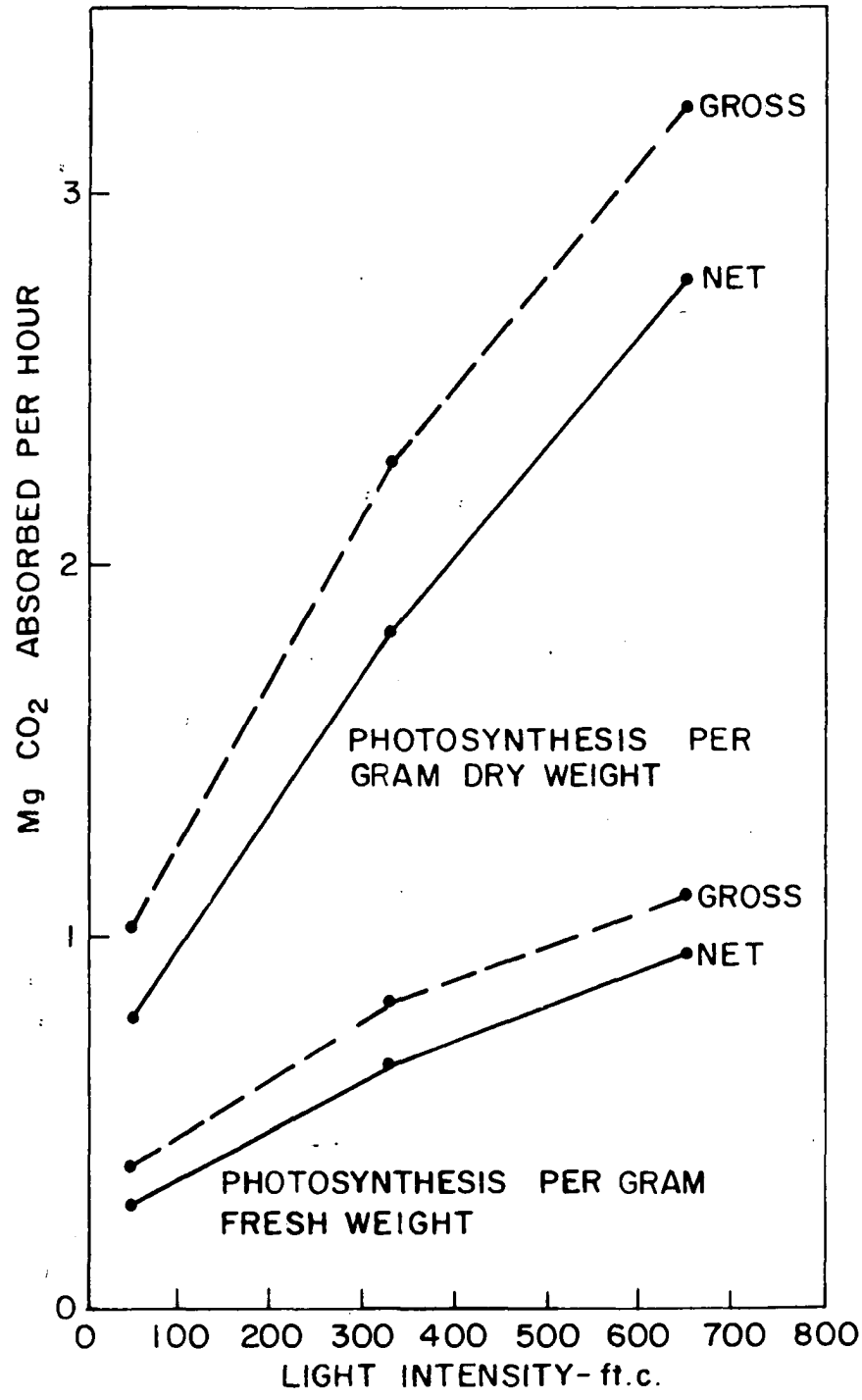

NET Ps PER GRAM FRESH WT.
NET Ps PER GRAM DRY WT.
Mg CO_2 ABSORBED PER HOUR
LIGHT INTENSITY - ft.c. X 10^{-3}
400
300
400
200
300
200
0
1
2
3
4
5
6
7
8
9
10

Figure 14. The relationship between rate of net and gross photosynthesis per gram of fresh and dry weight of needles and light intensity, (400 ppm CO_2).


GROSS
NET
PHOTOSYNTHESIS PER GRAM DRY WEIGHT
GROSS
NET
PHOTOSYNTHESIS PER GRAM FRESH WEIGHT
Mg CO_2 ABSORBED PER HOUR
0
1
2
3
0 100 200 300 400 500 600 700 800
LIGHT INTENSITY- ft.c.

Over the 1,200 to 2,400 foot-candle range, rate of dark respiration expressed on any base increased linearly with preceding light intensity (Table 13). The experiment with light intensities of 3,000, 6,000 and 9,000 foot-candles showed no effect of preceding light intensity on dark respiration (Table 11).

Effect of temperature

Mean needle temperature increased slightly with light intensity over the 3,000 to 9,000 foot-candle range, although ambient temperature did not. Mean needle temperature was 4.3°C higher in light than dark at an ambient temperature of 5°C, and 5.8°C higher in light than dark at an ambient temperature of 15°C. Mean needle temperatures resulting from the two ambient temperature treatments of 5°C and 15°C were 10.5°C and 19.3°C in light and 6.2°C and 14.5°C in dark.

CO_2 compensation point increased from 130 to 171 ppm as needle temperature increased from 10.5°C to 19.3°C, and time to reach CO_2 compensation point decreased from 162 to 118 minutes over the same range of needle temperature (Table 16). Water loss during measurement at the higher temperature was approximately double that at the lower temperature (Table 16). Rates of net and gross photosynthesis increased with an increase in needle temperature at a CO_2 concentration of 400 ppm (Figure 15). The Q_{10} of the rate of net photosynthesis was 1.6 on a seedling basis, and 2.1 on a gram fresh or dry weight of needle basis. However, rate of net photosynthesis was unaffected by temperature at a CO_2 concentration of 300 ppm (Figure 15). Rate of gross photosynthesis

Figure 15. The relationship between rate of net photosynthesis per gram fresh and dry weight of needles and mean needle temperature, for three CO_2 concentrations (400, 300 and 200 ppm).

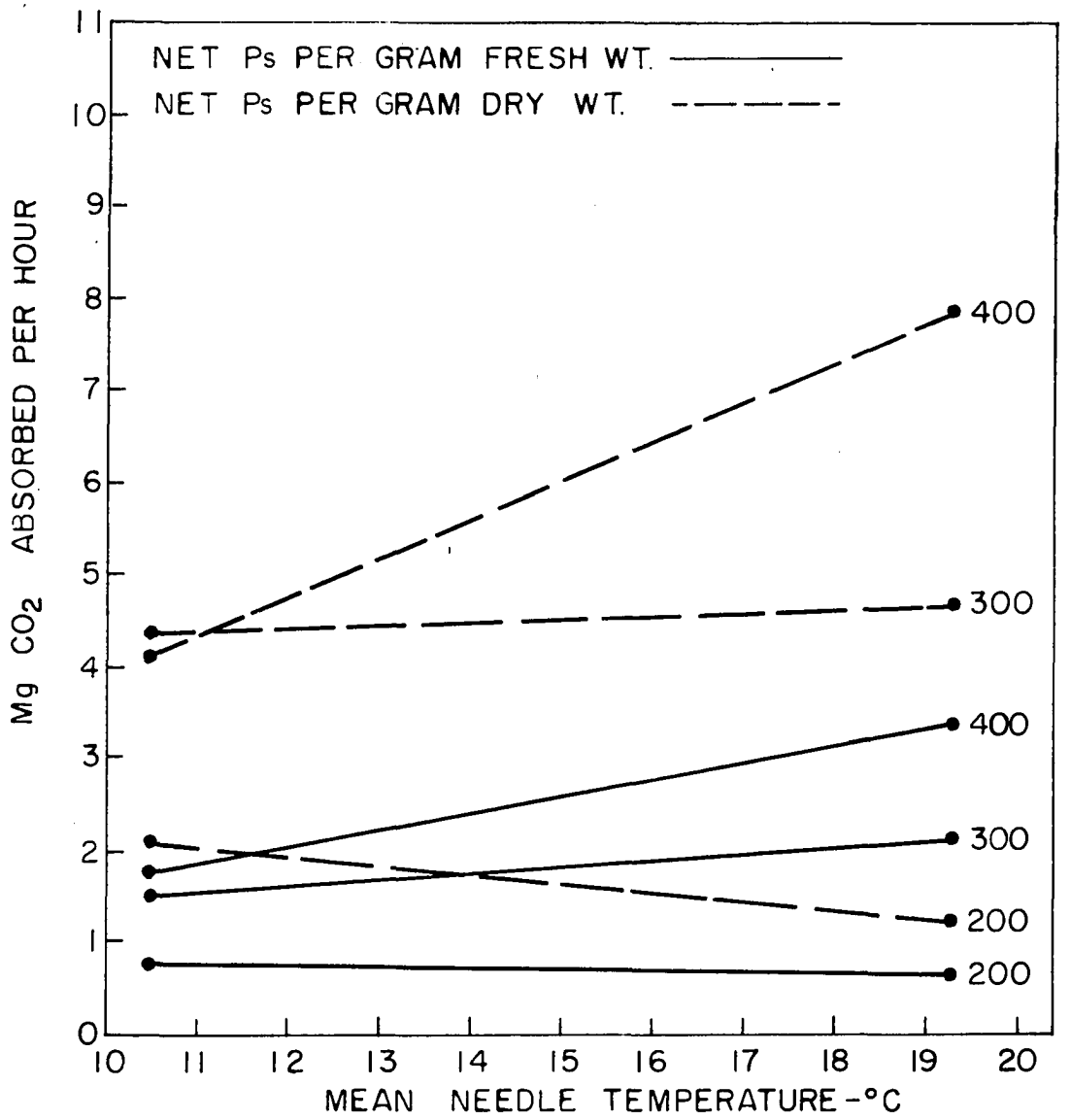

NET Ps PER GRAM FRESH WT.
NET Ps PER GRAM DRY WT.
Mg CO_2 ABSORBED PER HOUR
MEAN NEEDLE TEMPERATURE - °C
400
300
400
300
200
200
0
1
2
3
4
5
6
7
8
9
10
11
10
11
12
13
14
15
16
17
18
19
20

Figure 16. The relationship between rate of net and gross photosynthesis per seedling and mean needle temperature, for three CO_2 concentrations (400, 300 and 200 ppm).

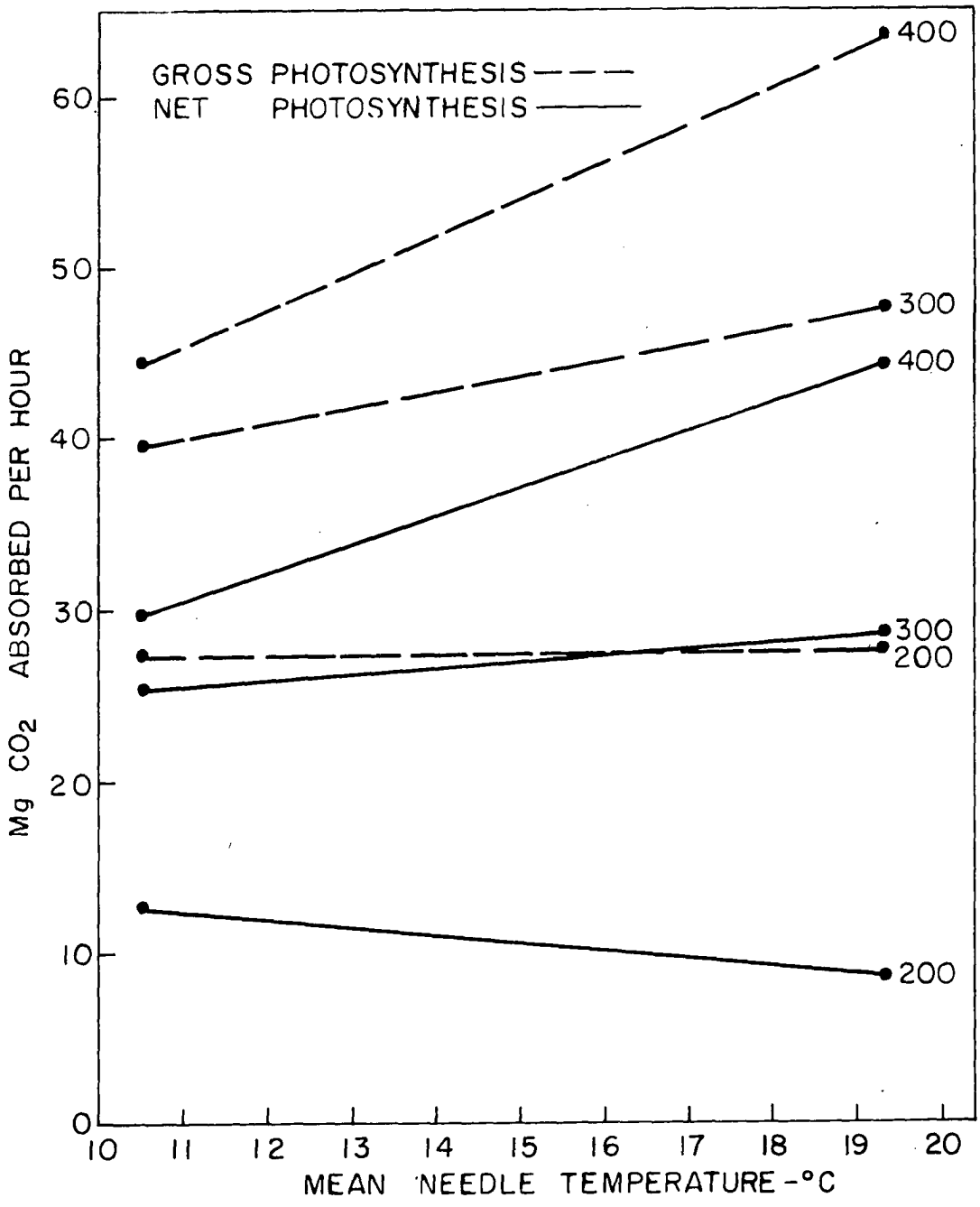

GROSS PHOTOSYNTHESIS
NET PHOTOSYNTHESIS
400
300
400
300
200
200
60
50
40
30
20
10
0
10
11
12
13
14
15
16
17
18
19
20
Mg CO2 ABSORBED PER HOUR
MEAN NEEDLE TEMPERATURE - °C

Figure 17. The relationship between rate of dark respiration per gram fresh and dry weight of needles and mean needle temperature.

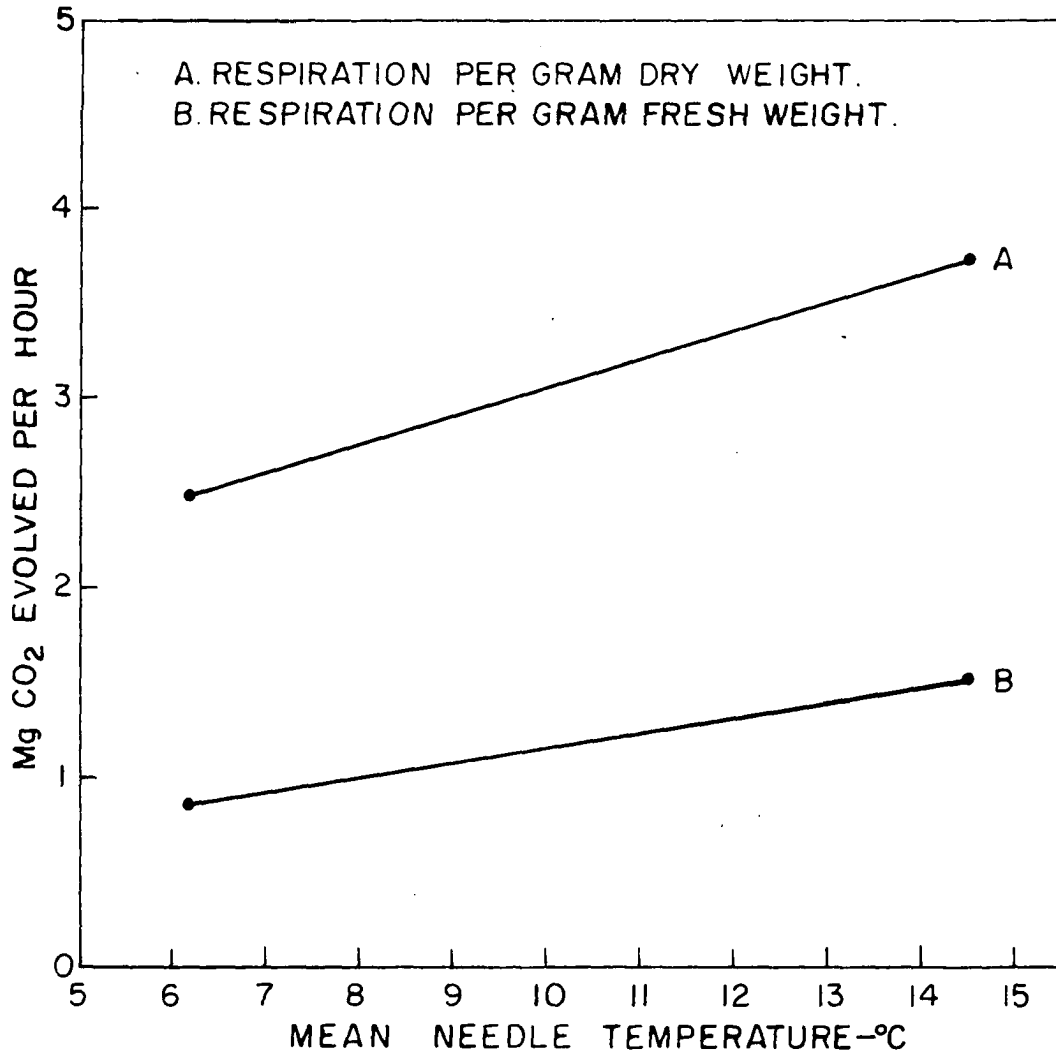

A. RESPIRATION PER GRAM DRY WEIGHT.
B. RESPIRATION PER GRAM FRESH WEIGHT.
A
B
Mg CO_2 EVOLVED PER HOUR
0
1
2
3
4
5
5
6
7
8
9
10
11
12
13
14
15
MEAN NEEDLE TEMPERATURE–°C

Table 16. Mean CO_2 compensation points, times to reach CO_2 compensation point and transpiration values for two mean needle temperatures

Needle temp.	CO_2 compensation point	Time to reach CO_2 compensation point	Transpiration
^oC	ppm CO_2	min.	g H_2O
10.5	130	162	7.4
19.3	171	118	15.6

increased with temperature at the 300 ppm CO_2 concentration, thus reflecting an increase in respiration rate with temperature (Table 11). At a CO_2 concentration of 200 ppm, rates of net photosynthesis per seedling and per gram dry weight of needles decreased with an increase in temperature (Figures 15 and 16). Rates of gross photosynthesis were unaffected by temperature at this CO_2 concentration (Figure 16). Rate of dark respiration increased with an increase in needle temperature (Figure 17). The Q_{10} of dark respiration was 1.4 on a seedling basis, 2.0 on a gram fresh weight of needle basis and 1.6 on a gram dry weight of needles basis.

DISCUSSION

Growth and Distribution of Assimilate

Effect of seed source

Marked differences in growth among seed sources were exhibited by first- and second-year seedlings. For first-year seedlings, total height, total fresh and dry weights, and fresh and dry weights of top and needles exhibited a curvilinear relationship with latitude of seed source, and calculated growth maxima occurred between 47^{o} and 50^{o}. In this range of latitudes, maximum daylengths are close to 16 hours, the artificially extended daylength under which the seedlings were grown. For fresh and dry weights of stem and roots, the relationship with latitude was not as strongly curved, thus indicating that daylength exerted a lesser influence on these variables. Production of juvenile needles was not as closely related to daylength as production of mature needles. Fresh and dry weight of juvenile needles varied less with latitude than did fresh and dry weight of mature needles, and the relationship with latitude was linear. Optimum shoot-root ratio is lower than the maximum obtainable under a given daylength; shoot-root ratio was maximum at a latitude south of the latitude of maximum growth. An early differential response to daylength was indicated by the sample of seedling tops and heights measured during the growth period, which showed that the latitudinal growth pattern was established at least two months before harvest.

The latitudinal growth pattern exhibited by the first-year seed-

lings was, in general, comparable to the second-year pattern. The central European seed sources from 50^{o} and 54^{o} grew more in height and produced more fresh and dry weight than the northern European source (60^{o}). However, the central European source from 54^{o} reached a slightly larger size by the second year than the source from 50^{o}, a reversal of the first-year trend. The initial influence of daylength was probably modified more strongly by other influences during the second year, thus producing a weaker relationship of second-year growth to latitude of seed source.

A simple relationship is commonly assumed to exist between the environment of an adapted genotype and the behavior of that genotype when subjected to a different environment. The validity of this assumption has been demonstrated for certain growth characteristics of Scotch pine seedlings by this study. Latitude is strongly related to daylength and less strongly related to temperature and integral solar radiation, which often are modified by altitude, atmospheric conditions, proximity to large bodies of water and other factors. Logically, then, the relationship of a given growth variable to latitude of seed source is assumed to be a measure of the relationship of the variable to daylength.

Departures from the linear or curvilinear relationship with latitude of seed source perhaps represent significant modifications of daylength adaptation by regional conditions. Thus, change in response caused by latitude of parent environment appears to be more rapid north than south of the Baltic. This difference may be caused by the steeper gradients of temperature and length of growing season north of the

Baltic then in central Europe. Unfortunately, this study did not include enough southeastern European seed sources to warrant generalization about this region.

On the basis of these departures from general daylength adaptation, northern and central "ecotypes" of Scotch pine for Eastern Europe could be hypothesized. However, unless a specific purpose exists for doing so, such operations are idle. For the growth variables measured, variation was continuous, but rate of variation differed with respect to latitude within each region. If, therefore, a clinal or an ecotypic description of genetic variation in Scotch pine must be chosen, these data support the former. However, as age increases, the genetic material selected by regional influences may become increasingly important physiologically, and the growth behavior of seedlings from latitudinally disparate origins within the same climatic region may become similar, thereby obscuring earlier growth differences due to selection under different daylengths.

Photosynthesis and Respiration

Effect of seed source

Rates of photosynthesis per seedling varied among seed sources for both first- and second-year seedlings, but rates of photosynthesis per gram fresh and dry weight of needles varied with seed source in first-year seedlings only. Fewer seed sources (three as opposed to eight) were included in the second-year study, and they spanned a narrower range of latitudes. Moreover, with increased needle quantity and aver-

age needle age, the influence of genotype on rate of photosynthesis per unit of needle weight probably became smaller relative to environmental influences.

Rates of photosynthesis per seedling in first-year seedlings were related in a curvilinear fashion to latitude of seed source, and calculated maximum rates occurred in the same range of latitudes (50^{o} to 47^{o}) as did maximum needle growth. In the second year, maximum rates of photosynthesis per seedling again occurred in the seed source (54^{o}) which produced maximum needle weight. For first-year seedlings, discontinuities in the relationship between latitude of seed source and rate of photosynthesis per seedling occurred at the same latitudes as did the discontinuities in the growth relationships previously discussed, but were more pronounced.

Rates of photosynthesis per gram fresh and dry weight of needles were minimum at approximately the same latitude that needle weight was maximum. Thus, a smaller portion of the total needle weight was photosynthetically active when produced under optimum daylength conditions. Perhaps seedlings, in which growth was retarded by improper daylength, did not initially produce new needles at as great a rate as those adapted to the prevailing daylength, and thus produced less total photosynthate over any given interval of time. Distribution of the photosynthate that was produced in the nonadapted seedlings also probably did not favor maximum needle development. The photosynthate that was available to the needles would have been used principally in the maintenance of existing protoplasm. The quantity of residual photosynthate

left for starch storage thus would have been smaller for the nonadapted seedlings, and perhaps needle cell walls were thinner. Therefore, the ratio of photosynthesizing protoplasm to starch, cell wall, and non-photosynthetic protoplasm was greater in the nonadapted seedlings, and they fixed more CO_2 per unit needle weight than did the adapted seedlings.

The seed source which grew most fixed the least rather than the most CO_2 per unit of leaf weight. This has implications for the tree breeder using physiological selection criteria. For Scotch pine seedlings, rate of photosynthesis per unit of needle weight was related to source of seed, and hence to genotype, but the relationship was not as anticipated. Thus an early, short-term selection program based on retaining seedlings exhibiting maximum rates of photosynthesis per unit of needle weight would, as indicated by these data, be a selection for minimum growth rates.

Effect of environmental factors

Light intensity and temperature affected rates of net and gross photosynthesis in the second-year seedlings, but did not interact with each other. Light intensity and temperature interacted with CO_2 concentration.

Rates of net and gross photosynthesis in first- and second-year seedlings showed little response to light intensity over the 3,000 to 9,000 foot-candle range, at a CO_2 concentration of 400 ppm. If the results of the three experiments of Study II are pooled, light saturation of photosynthesis occurs at or below 1,200 foot-candles. This result differs from the findings of Stålfelt (1924) and Decker (1957) who

found that rate of photosynthesis in Scotch pine increased with light intensity up to full sunlight. Two factors may account for this difference; (1) the greenhouse in which the seedlings in the present studies were grown was shaded during the month before rates were measured, and (2) 400 ppm is a higher CO_2 concentration than was employed by either of the other workers. Probably, needle temperature was lower in these experiments than in those of Stålfelt and Decker. However, at the lower CO_2 concentrations employed in the experiments of Stålfelt and Decker, the effect of temperature should not have been important.

Light compensation point at a CO_2 concentration of 400 ppm appeared to be less than 50 foot-candles. When the line of best fit for the lowest three light intensities employed (50, 350, and 650 foot-candles) was extrapolated to zero light intensity to estimate light compensation point, a positive value for net photosynthesis was obtained. No explanation of this behavior is available.

At CO_2 concentrations of 300 and 200 ppm, rate of photosynthesis increased with light intensity over the 3,000 to 9,000 foot-candle range, in agreement with the findings of Stålfelt and Decker. These results, when pooled with the 400 ppm CO_2 results, imply that light saturation intensity decreased when CO_2 concentration increased. Rabinowitch (1951) suggested that the imposition of a ceiling on the photosynthetic process by a third factor or complex of factors could explain results of this type. Temperature was the most probable limiting third factor in these experiments. However, Chapman and Loomis (1953) and others have found that light saturation intensity increased with increased CO_2 concentra-

tion, in species other than Scotch pine.

Increased needle temperature increased rates of photosynthesis only at the 400 ppm CO_2 concentration. At lower CO_2 concentrations, rate of the dark reaction was apparently limited so severely by CO_2 concentration that temperature had no effect. At the lowest CO_2 concentration (200 ppm), rate of photosynthesis was low enough, relative to rate of respiration, that the increase in respiration rate, caused by the increase in temperature, significantly lowered rate of net CO_2 fixation.

Temperature and light intensity affected CO_2 compensation point and time to reach CO_2 compensation point. An increase in needle temperature increased transpiration during the measurement period, but increased light intensity did not increase transpiration except as it affected needle temperature. CO_2 compensation point decreased with increasing light intensity, up to 9,000 foot-candles, the highest intensity used. Light intensity had no effect on time to reach CO_2 compensation point. An increase in temperature increased CO_2 compensation point and decreased time to reach CO_2 compensation point. These results indicate that CO_2 compensation point is determined by light intensity and temperature. Rate of photosynthesis decreased with decreasing CO_2 concentration until rates of photosynthesis and respiration were balanced. At low CO_2 concentrations, temperature did not affect rate of photosynthesis but did affect rate of respiration. An increase in temperature, therefore, should increase CO_2 compensation point. Increased light intensity increases rate of photosynthesis, but presumably does not affect rate of respiration proportionally; thus, CO_2 compensation point should decrease. CO_2 compensation point should be

lowest when a plant is exposed to high light intensity and low temperature. In nature, however, high light intensities and high needle temperatures usually occur together; therefore, average field CO_2 compensation points during the growing season should be high and should vary with the intensity of solar radiation. At a light intensity of 3,000 foot-candles and the relatively low needle temperature of 19.3°C, CO_2 compensation point was approximately 170 ppm. Possibly, on hot summer days, field CO_2 concentrations might fall to values near or below CO_2 compensation point for Scotch pine seedlings. Partial shade, which reduces needle heating caused by solar radiation, but which does not reduce rate of photosynthesis proportionally, should result in increased utilization of CO_2.

Rates of dark respiration increased with an increase in preceding light intensities over the 50 to 650 foot-candle range. This increase probably was caused by increased quantities of needle sugar that were available as respiratory substrate because of increased rates of photosynthesis in the preceding light period. However, an inductive effect of light intensity on respiration, not directly associated with sugar production, may also account for this response. The existence of such an inductive effect was indicated by the significant increase in rates of respiration over the 1,200 to 2,400 foot-candle range with no increase in rates of net photosynthesis.

Seed source-environmental factor interactions

Unexpectedly, the only interacting effects of seed source and light intensity on rates of photosynthesis and respiration occurred in

first-year seedlings and were confined to the northernmost seed sources (62^{o} and 66^{o}). These sources were affected oppositely by light intensities above 3,000 foot-candles. No explanation for this is available. Because the interacting effects of seed source and environmental factors other than light intensity on rates of photosynthesis and respiration were small or nonexistent in these experiments, environmental factors probably must interact with genotype over a considerable time before they exert a measurable combined influence.

LITERATURE CITED

Baker, F. S. 1950. Principles of silviculture. New York, New York, McGraw-Hill Book Co., Inc.

Bjurman, B. 1959. Photosynthesis in diploid and tetraploid Ribes satigrum. Physiologia Plantarum 12: 183-187.

Bonner, J. and J. Liverman. 1953. Hormonal control of flower initiation. In Loomis, W. E., ed. Growth and differentiation in plants. pp. 283-304. Ames, Iowa, Iowa State College Press.

Bormann, F. H. 1957. The relationship of ontogenetic development and environmental modification to photosynthesis in Pinus Taeda seedlings. In Thimann, K. V., W. B. Critchfield and M. H. Zimmermann, eds. The physiology of forest trees. pp. 197-215. New York, New York, The Ronald Press Co.

Bourdeau, P. F. 1958a. Photosynthesis and respiration rates in leaves of male and female quaking aspens. Forest Science 4: 331-334.

Bourdeau, P. F. 1958b. Photosynthesis behavior of sun- and shade-grown leaves of certain tolerant and intolerant tree species. (Abstract) Bulletin of the Ecological Society of America 39: 84.

Bourdeau, P. F. 1958c. Relation between growth and unit rate of photosynthesis. Northeastern Forest Tree Improvement Conference Proceedings 5: 58-62.

Bourdeau, P. F. 1963. Photosynthesis and respiration of Pinus strobus L. seedlings in relation to provenance and treatment. Ecology 44: 710-716.

Bourdeau, P. F. and F. Mergen. 1959. Photosynthesis and respiration in colchicine induced polyploid seedlings of slash pine. Journal of Forestry 57: 191-193.

Broerman, B. F. S., G. R. Gatherum and J. C. Gordon. 1966. A controlled environment chamber for use in measurement of gas exchange of tree seedlings. Unpublished manuscript in possession of J. C. Gordon. Ames, Iowa, Forestry Department, Iowa State University of Science and Technology.

Chapman, H. W. and W. E. Loomis. 1953. Photosynthesis in the potato under field conditions. Plant Physiology 28: 703-716.

Clark, J. 1961. Photosynthesis and respiration in white spruce and balsam fir. State University of New York, College of Forestry Technical Publication 85.

Decker, J. P. 1944. Effect of temperature on photosynthesis and respiration in red and loblolly pines. Plant Physiology 19: 679-688.

Decker, J. P. 1954. Effect of light intensity on photosynthetic rate in Scotch pine. Plant Physiology 29: 305-306.

Decker, J. P. 1957. Further evidence of increased CO_2 production accompanying photosynthesis. Journal of Solar Energy, Science and Engineering 1: 30-33.

Decker, J. P. 1959. Some effects of temperature and carbon dioxide concentration on photosynthesis of Mimulus. Plant Physiology 34: 103-107.

Echols, R. M. 1958. Variation in tracheid length and wood density in geographic races of Scotch pine. Yale University School of Forestry Bulletin 64.

Freeland, R. O. 1944. Apparent photosynthesis in some conifers during winter. Plant Physiology 19: 179-185.

Gerhold, H. D. 1959. Seasonal variation of chloroplast pigments and nutrient elements in the needles of geographic races of Scotch pine. Silvae Genetica 8: 113-123.

Gordon, J. C. and M. Hagman. 1966. Rates of photosynthesis in Scotch pine seedlings from different seed sources under low light intensities. Unpublished manuscript in possession of J. C. Gordon. Ames, Iowa, Department of Forestry, Iowa State University of Science and Technology.

Huber, B. and H. Polster. 1955. Zur Frage du physiologischen Ursachen der unterschiedlichen Stofferzeugung von Pappelklonen. Biologischen Zentralblatt 74: 370-420.

Iwanoff, L. A. and N. L. Kossowitch, 1929. Über die Arbeit der Assimilation-apparatus verschiedener Baumarten. I. Die Kiefer (Pinus sylvestris). Planta 8: 427-464.

Jensen, K. F. and G. E. Gatherum. 1965. Effects of photoperiod, temperature and provenance on growth and development of Scotch pine seedlings. Forest Science 11: 189-199.

Kendall, W. A. and N. L. Taylor. 1963. Rates of respiration and photosynthesis in clones of red clover. Crop Science 3: 146-147.

Kozlowski, T. T. 1949. Light and water in relation to growth and competition of Piedmont forest tree species. Ecological Monographs 19: 207-231.

Kozlowski, T. T. 1957. Effect of continuous high light intensity on photosynthesis of forest tree seedlings. Forest Science 3: 220-224.

Kozlowski, T. T. and C. H. Winget. 1964. The role of reserves in leaves, branches, stems, and roots on shoot growth of red pine. American Journal of Botany 51: 522-529.

Kramer, P. J. 1957. Photosynthesis of trees as affected by their environment. In Thimann, K. V., W. B. Critchfield and M. H. Zimmermann, eds. The physiology of forest trees. pp. 157-186. New York, New York, The Ronald Press Co.

Kramer, P. J. and W. S. Clark. 1947. A comparison of photosynthesis in individual pine needles and entire seedlings at various light intensities. Plant Physiology 22: 51-57.

Kramer, P. J. and J. P. Decker. 1944. Relation between light intensity and rate of photosynthesis of loblolly pine and certain hardwoods. Plant Physiology 19: 350-357.

Kramer, P. J. and T. T. Kozlowski. 1960. Physiology of trees. New York, New York, McGraw-Hill Book Company, Inc.

Krotkov, G., V. C. Runeckles and K. V. Thimann. 1958. Effect of light on the CO_2 absorption and evolution by Kalanchoe, wheat and pea leaves. Plant Physiology 33: 289-292.

Krueger, K. W. and W. K. Ferrell. 1962. Photosynthesis and respiration rates of Douglas fir seedlings from a coastal and a Rocky Mountain seed source. Bulletin of the Ecological Soceity of America 43: 8.

Ladell, J. L. 1963. Needle density, pith size, and tracheid length in pine. University of Oxford, Commonwealth Forestry Institute. Institute Paper 36.

Langlet, O. 1936. Studier över tallens fysiologiska variabilitet och dess samband med klimatet. Meddelanden från Statens Skögsförsöksanstalt i Stockholm 29: 219-470.

Langlet, O. 1943. Photoperiodismus und Provenienz bei der gemeinen Kiefer (Pinus sylvestris L.). Meddelanden från Statens Skogsförsöksanstalt i Stockholm 33: 295-330.

Langlet, O. 1959. A cline or not a cline - a question of Scots pine. Silvae Genetica 8: 13-22.

Larson, P. R. 1964. Contribution of different-aged needles to growth and wood formation of young red pines. Forest Science 10: 224-237.

McGregor, W. H. D., R. M. Allen and P. J. Kramer. 1961. The effect of photoperiod on growth, photosynthesis and respiration of loblolly pine seedlings from two geographic sources. Forest Science 7: 342-343.

Mooney, H. A. and W. D. Billings. 1961. Comparative physiological ecology of arctic and alpine populations of Oxyria digyna. Ecological Monographs 31: 1-29.

Negisi, K. and T. Satoo. 1961a. Effect of air supply on apparent photosynthesis of akamateu (Pinus densiflora Sieb. et Zucc.), sugi (Cryptomeria japonica D. Don.) and kinoki (Chamaecyparis obtusa Sieb. et Zucc.), (English summary). Journal of the Japanese Forestry Society 43: 354-355.

Negisi, K. and T. Satoo. 1961b. Effect of temperature on photosynthesis and respiration of akamatu (Pinus deusiflora Sieb. et Zucc.), sugi (Cryptomeria japonica D. Don.) and kinoki (Chamaecyparis obtusa Sieb. et Zucc.) (English summary). Journal of the Japanese Forestry Society 43: 336-343.

Negisi, K., H. Yameguchi, K. Yagi and T. Satoo. 1961. Photosynthesis of sugi (Cyptomeria japonica) in early spring (English summary). Journal of the Japanese Forestry Society 43: 233-240.

Ovington, J. D. 1962. Quantitative ecology and the woodland ecosystem concept. Advances in Ecological Research 1: 103-192.

Parker, J. 1961. Seasonal trends in carbon dioxide absorption, cold resistance and transpiration of some evergreens. Ecology 42: 372-380.

Pavletic, Z. and H. Lieth. 1958. Der Lichtkompensationspunkt einiger immergruner Pflanzen im Winter und im Fruhjahr. Berichte der Deutschen Botanischen Gesellschaft 71: 309-314.

Pharis, R. P. and F. W. Woods. 1960. Effects of temperature upon photosynthesis and respiration of Choctawhatchee sand pine. Ecology 41: 797-799.

Pisek, A. and G. Rehner. 1958. Temperaturminima der Netto-Assimilation von mediterranen und nordisch-alpinen Immergrunen. Berichte der Deutschen Botanischen Gesellschaft 71: 188-193.

Pisek, A. and E. Winkler. 1959. Licht - und temperaturabhängegkeit der CO_2 -Assimilation von Fichte (Picea excelsa Link.), Zirbe (Pinus cembra L.) und Sonnenblume (Helianthus annuus L.). Planta 53: 532-550.

Polster, H. and G. Weisse. 1962. Vergleichende Assimilationsuntersuch - ungen an Klonen verschiedener Lärchenherkünfte (Larix decidua and Larix leptolepis) unter Freiland - und Klimaraumbedingungen. Der Zuchter 32: 103-110.

Rabinowitch, E. I. 1951. Photosynthesis and related processes. Volume 2, Part 1. New York, New York, Interscience Publishers, Inc.

Rusch, J. 1959. Das Verhältnis von Transpiration und Assimilation als physiologische Kenngrösse, untersucht an Pappelklonen. Der Zuchter 29: 348-354.

Sirois, D. L. and G. R. Cooper. 1962. The influence of light intensity, temperature and atmospheric carbon dioxide concentration on rate of apparent photosynthesis of a mature apple tree. Maine Agricultural Experiment Station Bulletin 626.

Stålfelt, M. G. 1921. Till kännendomen om förhållandet mellan solbladens och skuggbladens kolhydratsproduction. Meddelanden från Statens Skogsförsöksanstalt i Stockholm 18: 221-230.

Stålfelt, M. G. 1924. Tallens och granens kolsyreassimilation och dess ekologiska betingelser. Meddelanden från Statens Skogsförsöksanstalt i Stockholm 21: 181-258.

Stout, B. B. 1964. Stem-crown relationships in Scotch pine. Northeastern Forest Tree Improvement Conference Proceedings 11: 31-35.

Thomas, M. D. 1965. Photosynthesis (carbon assimilation): environmental and metabolic relationships. In Steward, F. C., ed. Plant physiology. Volume 4A. pp. 15-67. New York, New York, Academic Press, Inc.

Thut, H. F. and W. E. Loomis. 1944. elation of light to growth of plants. Plant Physiology 19: 117-130.

Tonzig, S. and E. Marre. 1964. Comparative studies on the photosynthetic efficiencies of poplar hybrids, with investigation of the limiting factors. Institute of Plant Sciences, University of Milan. First Annual Report. Original not available; reprint secured from U. S. Forest Service, North Central States Forest Experiment Station, St. Paul, Minnesota.

Tranquillini, W. 1955. Die Bedeutung des Lichtes und der Temperature für die Kohlensaureassimilation vou Pinus cembra - Jungwuchs an einem hochalpinen Standort. Planta 46: 154-178.

Vaartaja, O. 1954. Photoperiodic ecotypes of trees. Canadian Journal of Botany 32: 392-399.

Wareing, P. F. 1950. Growth studies in woody species. I. Photoperiodism in first year seedlings of Pinus sylvestris. Physiologia Plantarum 3: 300-314.

Wareing, P. F. 1956. Photoperiodism in woody plants. Annual Review of Plant Physiology 7: 191-214.

Wassink, E. C. and S. D. Richardson. 1951. Observations on the connection between root growth and shoot illumination in first-year seedlings of Acer pseudoplatanus L. and Quercus borealis maxima (Marsh) Ashe. Koninkl. Nederlandsel. Akademie van Wetenschappen Proceedings Series C, 54, No. 5.

Wassink, E. C., S. D. Richardson and S. A. Pieters. 1956. Photosynthetic adaptation to light intensity in leaves of Acer pseudoplatanus. Acta Botanica Neerlandica 5: 247-256.

Watson, D. J. 1947. *Comparative studies on the growth of field crops.* Annals of Botany New Series 11: 41-76.

West, R. F. and F. T. Ledig. 1964. Lammas shoot formation in Scotch pine. Northeastern Forest Tree Improvement Conference Proceedings 11: 21-30.

Wright, J. W. and H. I. Baldwin. 1957. The 1938 international union Scotch pine provenance test in New Hampshire. Silvae Genetica 6: 2-14.

Wright, J. W. and W. I. Bull. 1963. Geographic variation in Scotch pine. Silvae Genetica 12: 1-25.

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